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Bulletin 11

"*Spirifer disjunctus*": Its Evolution and Paleoecology in the Catskill Delta

by

HUGO GREINER

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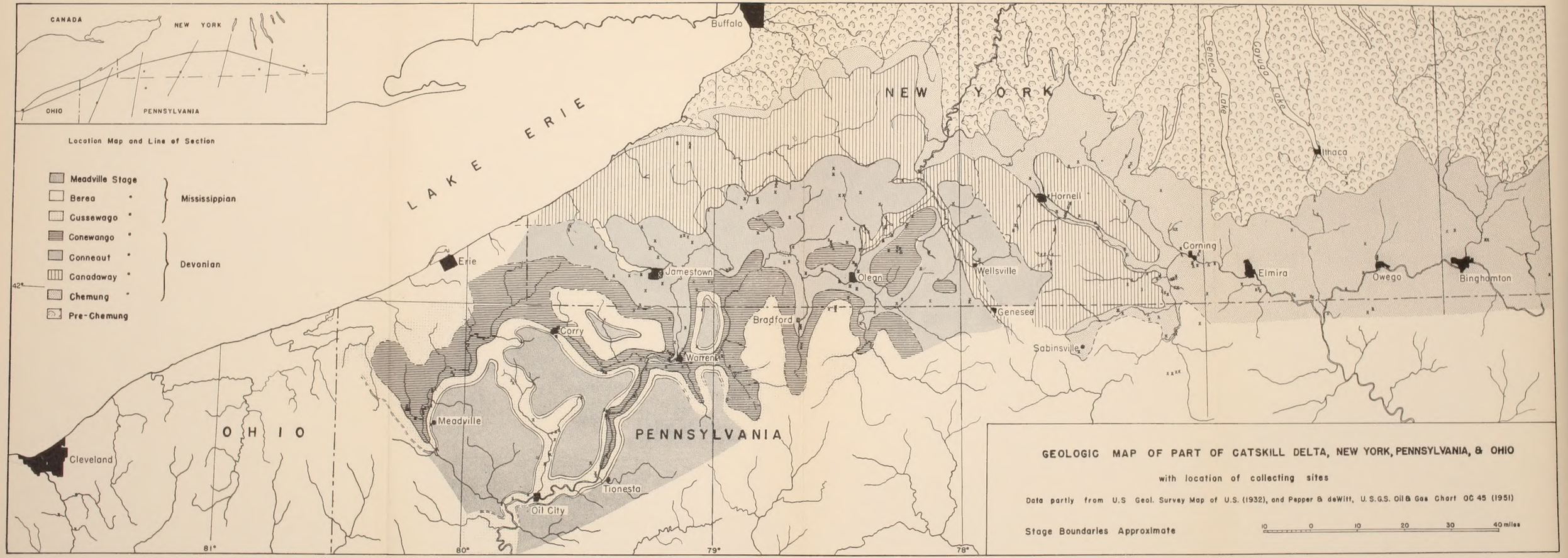

Fig. 1. Geologic map of part of the Catskill Delta showing position of collecting localities.

PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY

BULLETIN 11

"Spirifer disjunctus": Its Evolution and Paleoecology in the Catskill Delta

BY

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ABSTRACT

Much of the variation in the "*Spirifer disjunctus*" tribe of the Catskill Delta is found to be of taxonomic importance. In this group, 18 species of *Cyrtospirifer* are recognized, of which 13 are new. The stratigraphic range of each species in the standard section of the Upper Devonian and in the Lower Mississippian of New York and Pennsylvania is determined.

The paleoecology of these cyrtospirifers, as revealed in the litho- and biofacies, is studied, and the shell morphology is seen to be affected by the environment in which the animal lived; attenuate cyrtospirifers, for instance, are adapted to a shale facies. Faunal associates of the different species of *Cyrtospirifer* in each stage are determined.

The sudden appearance of this tribe in the Chemung Stage is interpreted as a migration from some other faunal province. This invasion had a profound effect on the faunal evolution in the Catskill Delta. Two other maximal periods of speciation, in late Canadaway-early Conneaut time, and again in early Conewango time, are considered to be mainly due to rapid expansion within local cyrtospiriferid groups in response to environmental change.

Two principal phyletic lines are recognized in the cyrtospirifers of the Appalachian province, and from these "step series" of related species evolved, five from the first and four from the second major "ancestral series." Evolutionary trends in the development of *Cyrtospirifer* are examined.

The abundance of individuals of the species and of the amount of speciation are estimated, and a lack of coincidence of the peaks for these two variables are noted.

INTRODUCTION

"*Spirifer disjunctus*" of authors is one of the most abundant and widespread elements of the Upper Devonian faunas of the Appalachian province, appearing abruptly at the base of the Chemung Stage and ranging upward through the higher Devonian beds and into the base of the Mississippian. In most of the literature it seems to have been considered a single highly variable species, but although often described or listed, it has not previously been subjected to monographic study.

The present research was undertaken to discover whether the protean forms of these spirifers represent merely random and meaningless variation or whether they are genetic units with limited distribution in time and significant restriction to particular ecologic facies.

The results prove that we are dealing not with a single variable species but with a tribe of genetically related species with well-defined characteristics, each having a limited stratigraphic range and some of them being adapted to special biotopes.

ACKNOWLEDGMENTS

This paper has been presented to the faculty of the Graduate School of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The work was undertaken at the suggestion of Dr. Carl O. Dunbar, to whom the writer is also deeply indebted for his helpful guidance in bringing the material to its present state of completion. The study has been made possible by the Charles Schuchert Memorial Fund from which the writer was awarded the Schuchert Fellowship in 1952–53 and from which the field work was financed. Many helpful suggestions have been graciously given by Drs. Joseph T. Gregory and Karl M. Waagé, both of Yale University. The photographic work was made possible through the able instruction of Mr. Percy A. Morris of Yale Peabody Museum.

The large fossil collections made in 1931 by Mr. E. I. Leith, presently of the University of Manitoba, Canada, were a source of many fine specimens. The use of Mr. Leith's field maps, with their locations of good fossil sites, greatly facilitated field collecting.

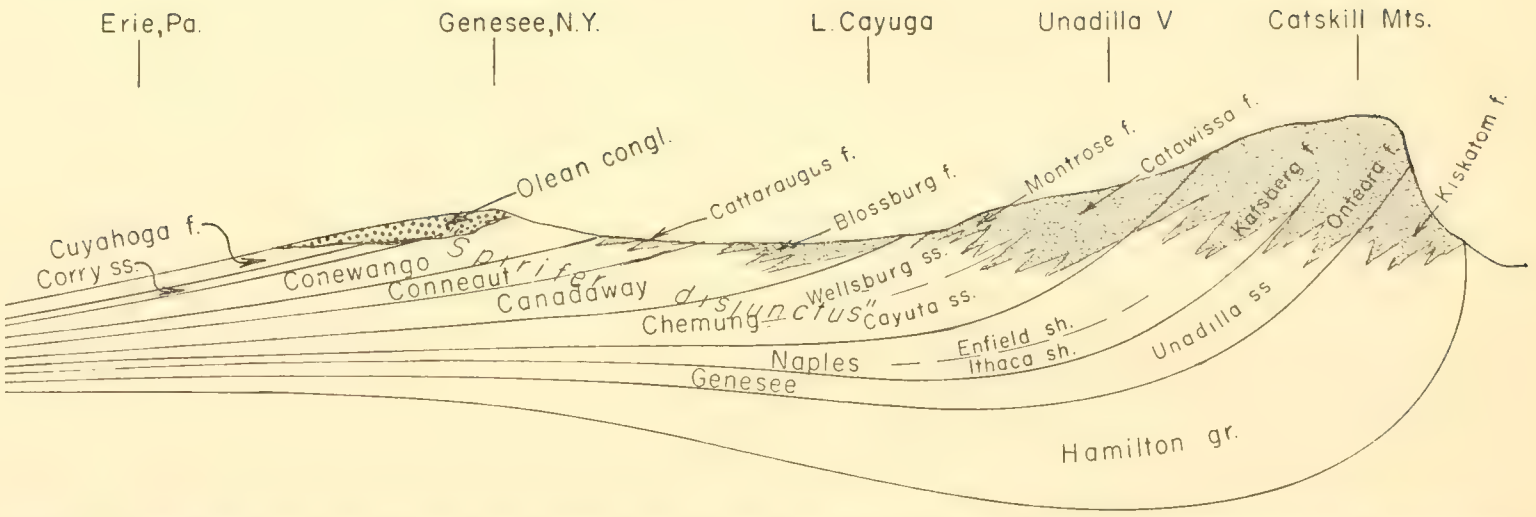


Fig. 2. Generalized cross section from Erie, Pennsylvania to the front of the Catskill Mountains showing general classification of the Middle and Upper Devonian formations of the Catskill Delta.

FIELD METHODS AND LABORATORY TECHNIQUE

During the summer of 1953, specimens of "*Spirifer disjunctus*" and its associated faunas were collected in a broad area extending from the neighborhood of Binghamton, New York, westward in a belt straddling the New York-Pennsylvania border to the general vicinity of Meadville, Pennsylvania (fig. 1). Most westerly of all, the fossiliferous uppermost beds of the Chagrin formation, in the Cleveland region of Ohio, which contain "*Spirifer disjunctus*," were sampled. Particular attention was paid to quadrangles in which the stratigraphy and paleontology had been well studied. The excellent topographic maps, which were constantly available, and the use of an altimeter, made the location of outcrops a pleasure, rather than a chore.

By concentrating on this well-exposed belt of strata, the entire sequence of formations could be thoroughly examined in a complete segment through the delta (fig. 2).

The study is based on several tons of richly fossiliferous specimens representing many localities and all the faunal zones in the Catskill Delta in which cyrtospirifers are present (fig. 3).

Most of the beds are abundantly fossiliferous, weathering to produce the beautiful molds and casts for which the region is geologically famous. In collecting, at many places, such a plethora of good, fossiliferous rock samples prevailed that the rule was made to preserve only what seemed to be an adequate sample. Where possible a specimen of both fresh and weathered material was obtained, and at all places attention was given to collecting all the available associated fossils as well. Extensive collections made by E. I. Leith in 1931 were also studied.

Although the best fossils occur as molds, it was easy to secure artificial casts, either in dental wax or latex. Not uncommonly, it was possible to get casts showing both the exterior and interior features of the same shell. Where the matrix is friable, it was first strengthened by impregnating it with alvar (a celluloid solution in acetone). In case the mold was deep or complicated so that a dental wax cast could not be freed, a rubber cast was made with liquid latex.

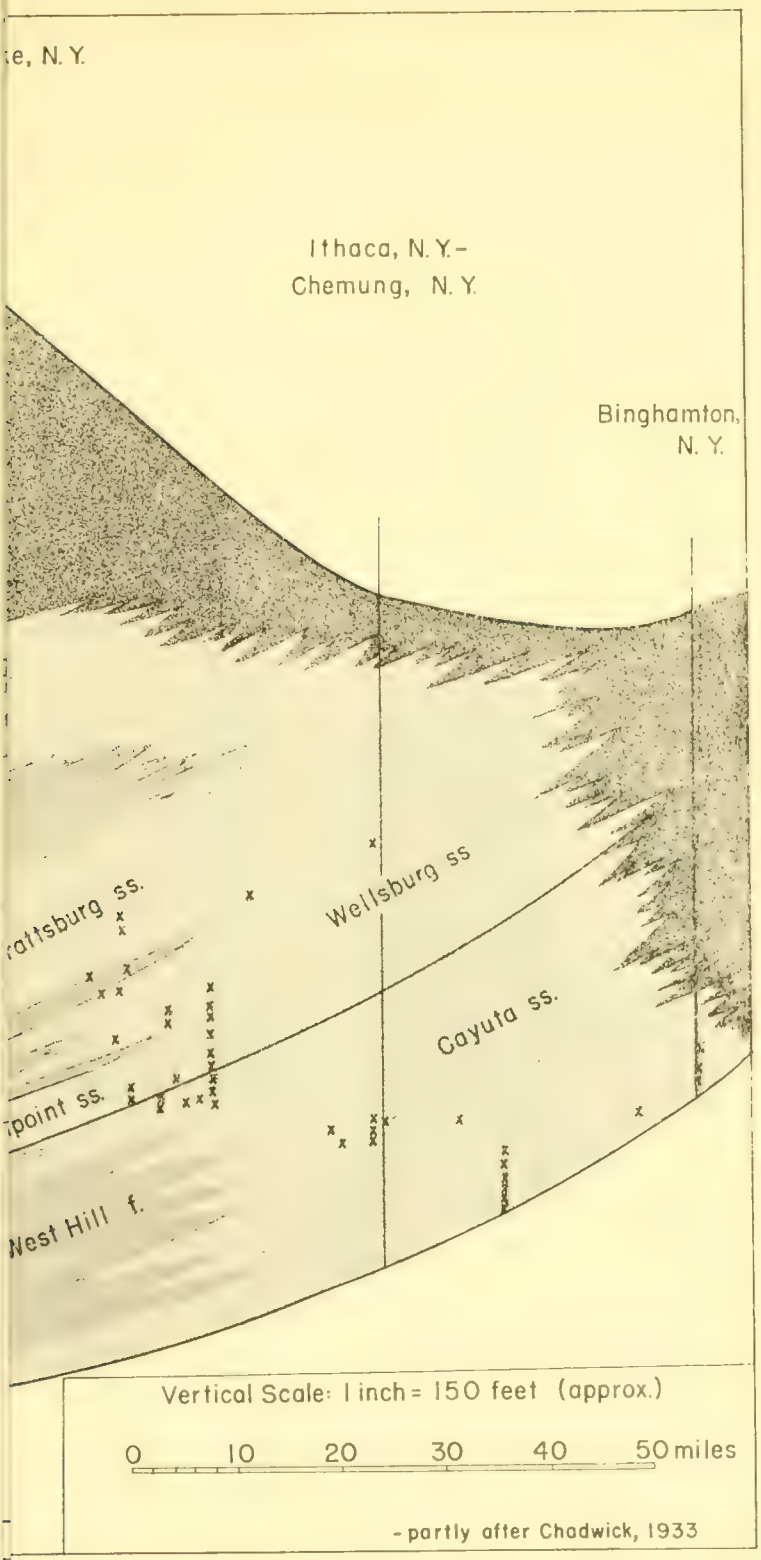
In making a dental wax cast, best results were obtained by using a mixture of equal amounts of both the red and the white impression compounds, for the latter used by itself is much too brittle.*

Liquid latex impressions were best obtained as follows: After thin application of a "separator," a very thin initial coating of "Pliatex" was applied to the mold with a brush, and allowed to harden very thoroughly. Several

* Dental wax is obtainable from Kerr Manufacturing Co., Detroit 8, Michigan, and liquid latex and separator from National Sculpture Services, 304 West 42nd Street, New York 18, New York.

further coatings, similarly applied and hardened, permitted a cast of sufficient thickness to be built up. Removal with tweezers was then very easy.

Both the casts and latex impressions were carefully and thinly painted with india ink, and, after drying, were coated with a patina of white magnesium oxide. This was done with the use of magnesium ribbon. A 2-inch section of the ribbon, doubled-up, grasped in tweezers, and ignited over an alcohol lamp, gave forth a mass of smoke which coated a cast held over it with a pure white oxide. The specimen was then ready for study or photographing.


Ithaca, N.Y.–
Chemung, N.Y.
Binghamton,
N.Y.
Wellsburg ss
Cayuta ss.
West Hill f.
Vertical Scale: 1 inch = 150 feet (approx.)
0 10 20 30 40 50 miles
- partly after Chadwick, 1933

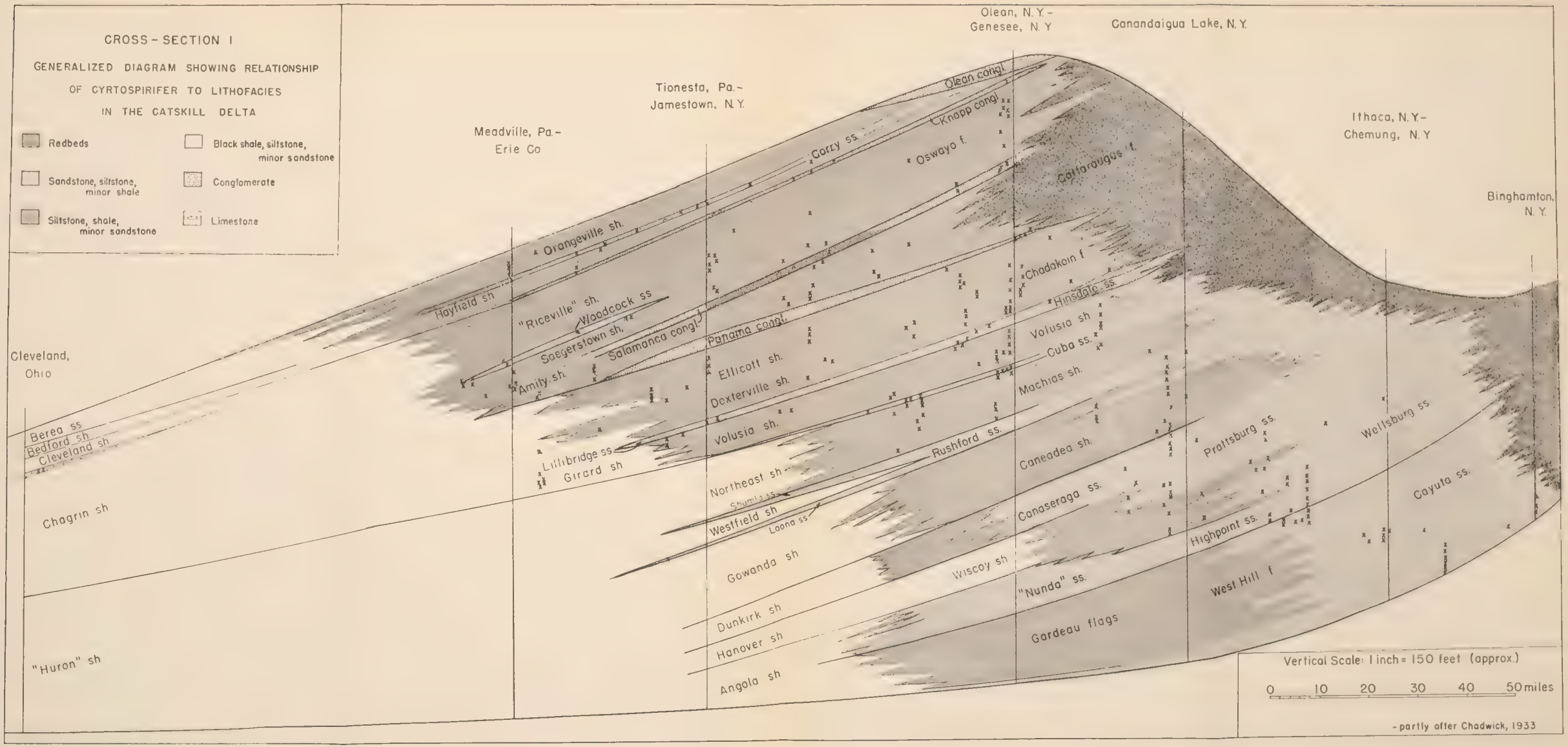


Fig. 3. Cross section of the Middle and Upper Devonian formations from near Binghamton, New York, to Cleveland, Ohio, showing lithologic facies and the position of all collecting points.

STRATIGRAPHIC SETTING

The "*Spirifer disjunctus*" tribe ranges through some 2500 feet of beds in the Upper Devonian and Lower Mississippian of New York and Pennsylvania. Here, during a span of perhaps 5 or 6 million years, it occupied a broad belt of shallow, sandy sea floor, hemmed in on the east by the shoreline and on the west by deeper water and muddy bottoms. Its favored environment shifted back and forth with fluctuations in growth of the Catskill Delta, but in general shifted farther and farther to the west. During this long span of time it must have tried to adapt itself to various niches in the environment. Here, then, in the extremely rich faunas of the Upper Devonian rocks, is the record of a vast experiment in adaptation.

"*Spirifer disjunctus*" appears suddenly at the base of the Chemung Stage of the Upper Devonian and ranges upward through the rest of the Devonian and into the base of the Mississippian in the Appalachian Trough. When it appeared, the Catskill Delta was already partly built, but the subaerial part, represented by the redbed facies, was then limited to about the eastern one-third of the trough—that is, to the region east of a north-south line running approximately through Binghamton, New York. With the progress of time, the subaerial part of the delta spread westward and the sublittoral, sandy facies likewise shifted so as to appear higher in the section but farther and farther west, as shown in figure 2.

The redbeds with their abundant mudcracks, traces of the roots of trees, cross-bedded sandy phases, general lack of marine fossils, and reddish color indicate deposition above sea-level, probably on a great alluvial plain. Doubtless numerous streams, having their sources in the uplifted Appalachian highlands to the east and southeast, dumped their loads of sand and silt upon the flood plain and onto deltas formed in the shallow seas at their mouths. The coalescence of a number of minor deltas built the vast, compound structure known as the Catskill Delta.

In front of the redbed facies, gray sandstones, siltstones, and shales, rich in marine fossils, represent deposits on the littoral and sublittoral parts of the delta. As might be expected, facies changes on both a large and small scale occur abruptly, in this part of the section. Individual sandstone beds several feet thick can be seen pinching out in a few tens of feet; cross-bedded channel-fillings abound; thin shale beds and partings break up even the thickest sandstone sequences. As if further evidence of their near-shore sites of deposition were needed, interfingering redbeds are generally near at hand, and the distinctive structures once known as flow rolls, which are probably due to near-shore slumping in freshly laid sediments, are conspicuous. A study of the litho- and biofacies in this part of the sequence has an advantage over other, equally fossiliferous, Paleozoic sections in that the

approximate location of the shoreline at any interval of the section can be determined.

It is the general type of deposit outlined above which was spoken of as "Chemung" by early geologists, and thought of as a single formation. Likewise, it was in these gray sandy and silty phases that "*Spirifer disjunctus*" found its most congenial environment. Together with the rather distinctive type of sedimentation, the presence of this fossil was considered final proof by early workers that they were dealing with "Chemung" strata. Similar facies of dissimilar stages were confounded one with another. In reality, these beds measure several thousands of feet in thickness and their period of deposition spans a vast interval of time.

Still farther to the west, a third major facies is found: the black shales of Ohio, Indiana, and Kentucky. These probably represent the fine-grained, muddy deposits laid down in deeper, quieter waters in front of the growing delta. In general, fossils are not common in the black shale facies and Cyrtospirifers are entirely lacking. Limestone beds are conspicuously absent throughout almost the entire thickness of strata. Although the seas of the time must have contained an abundance of calcium carbonate, as indicated by the great quantities of fossil shells commonly present, conditions for the deposition of limestones, other than occasional "coquinite" beds, did not exist. In the Volusia formation near Jamestown, in the western part of the Appalachian province, a few thin, fossiliferous limestone beds appear, but these remain so rare that even in the (Mississippian) Cussewago Stage, at its type area near Meadville, Pennsylvania, a few units of about one foot thickness are given member designation.

The sediments deposited on the delta also displayed variation in their lithic content over considerable geographic areas, and through intervals of time of varied length. These lithogenetic units make more-or-less distinctly recognizable formations, and the formations are grouped into larger stratigraphic units on the basis of their obvious relationships to other formations in the group. Distinct separation from formational groups lying above or below them, either by pronounced hiatuses, basal conglomerates, change of faunal and lithic content, or combinations of these characters, further sets them apart from one another.

George H. Chadwick, whose excellent work has greatly clarified our knowledge of the stratigraphy of the Catskill Delta, has recognized five stages in the Upper Devonian and Lower Mississippian of the Appalachian province. For easy reference, a synoptic view of the stratigraphy of this part of the geologic section for the area is given here. Data have been derived mainly from the works of Chadwick (1933) and Caster (1934).

The stages, being time-stratigraphic units, also represent the ages during which the deposits of which they are composed were laid down. As indicated in figure 2, the "*Spirifer disjunctus*" facies transgresses the boundaries of the stages. The rock formations which form the stages, however, may be traced through a number of different facies. Hence, by employing both

Cleveland, Ohio	*Meadville, Pa.-Jamestown, N.Y.*	*Olean-Genesee, N.Y.*	*Canandaigua, N.Y.*	*Ithaca-Chemung, N.Y.*	
	MISSISSIPPIAN SYSTEM:				
	—Waverlyan Subsystem—				
	Kinderhookian Series				
	Shenango Stage				
	Meadville Stage				
	Harvest Home sh.	Cuyahoga			
	Sharpsville ss.	Group			
	Orangeville sh.				
Berea	*Berea Stage*				
Bedford	Corry sandstone				
	Cussewago Stage				
	Hayfield shale				
	Tidioute shale				
	Knapp formational suite	Knapp formation			
Cleveland	Kushequa shale				
	(Marvin Creek Is.)				
	DEVONIAN SYSTEM:				
	Conewango Stage				
	"Riceville" fm.				
	Oswayo shale	Oswayo shale			
	Roystone coquinite	Roystone coq.			
	Woodcock sandstone				
	Saegerstown shale				
	Salamanca cgl.	Salamanca ss.			
	Amity shale	Cattaraugus sh.			
Chagrin sh.	Panama cgl.	Panama cgl.			
	Conneaut Stage				
	Ellicott shale	"Chadakoin"			
	Dexterville shale	fm.			
	Lillibridge ss.	Hinsdale ss.			
	Volusia (Girard) sh.	Volusia sh.			
	Cuba sandstone	Cuba sandstone			
	Canadaway Stage				
	Northeast sh.	Machias shale			
	(lower beds not	Rushford ss.			
"Huron"	exposed)	Caneadea sh.			
black		Canaseraga ss.	Pratts-		
shale		Wiscoy shale	burg sh.	Wellsburg ss.	
		Nunda ss.	Highpoint fm.		
		Gardeau sh.	West Hill fm.	Cayuta sh.	*Chemung Stage*
		Grimes ss.	Grimes ss.	and ss.	

facies and formation, every fossil collection can be placed accurately within space and time.

Having already observed that the *"disjunctus"* tribe showed a special preference for a particular marine facies, it is now necessary to look briefly at their second relationship: that to the time-rock units that make up the stratigraphic section (see fig. 3).

In the Ithaca-Chemung region, the Cayuta formation, which is the lower unit of the Chemung Stage, lies on the dark Upper Devonian Enfield shale, and consists of thin-bedded shales, and lenticular, locally cross-bedded siltstones and sandstones. In the upper unit, the Wellsburg formation, sandstone beds are much more abundant, and fossils, especially *"Spirifer disjunctus,"* are much scarcer. Cross-bedding and other near-shore features still prevail, however.

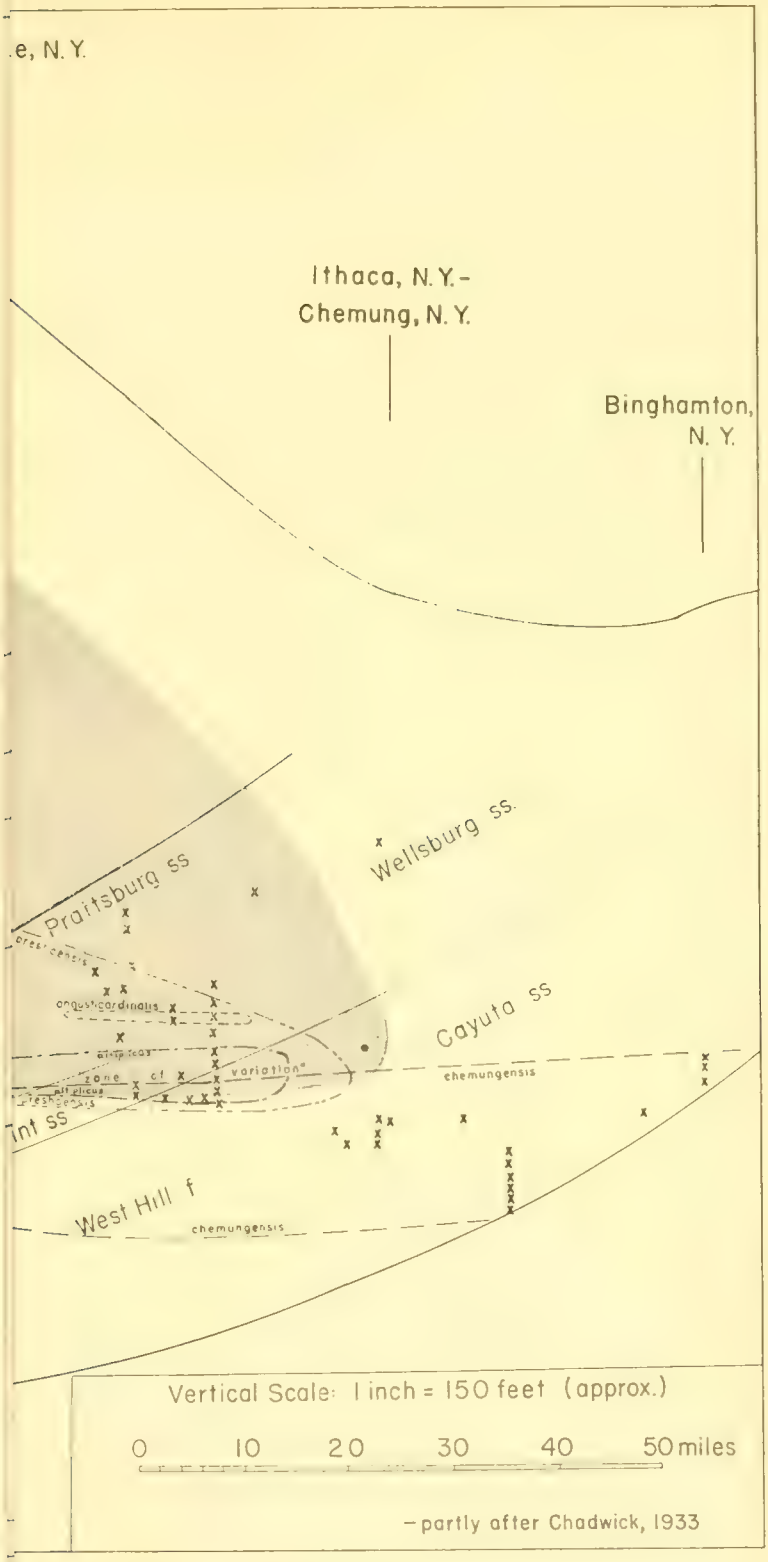
In the vicinity of Corning, New York, there is a slight but pronounced disconformity with thin redbeds below and conspicuous flow rolls in a sandstone and shale suite above. This has been taken to be the base of the Wiscoy formation at this locale. Some 10 feet below this hiatus, a 10-foot interval of bluish-colored shale and siltstone, with some unique faunal features, to be discussed later, has been found.

In the region of Hornell, New York, this same shale zone has been located, but the upper part of the Wiscoy formation has a higher content of shale in that area. The overlying Perrysburg formation consists largely of massive sandstone and siltstone beds in the lower part—the Canaseraga member—with the much more shaly Caneadea member above. These, with the overlying Rushford sandstone and Machias formation, comprise the Canadaway Stage.

At the base of the Conneaut Stage there is an extremely widespread although relatively thin, massive-bedded sandstone unit, the Cuba sandstone. Above this, the rest of the Conneaut Stage consists of a monotonous series of thin siltstones, sandstones, and gray shales, in which only the Hinsdale sandstone and a zone of dark purple or chocolate-weathering shales near the mid-section provide much variety.

The Panama conglomerate at the base of the Conewango Stage marks an important break both physical and faunal. This conglomerate has been traced from northeastern Ohio to the vicinity of Jamestown, New York, where it has its maximum thickness, and then eastward to beyond Olean, where it wedges out as several thin, conglomeratic beds only a few inches thick.

In the last-named neighborhood, the next higher formation in the Conewango Stage is the Cattaraugus, consisting of reddish and greenish shales and sandstones of the continental facies. This sequence is broken up near its mid-section by the Salamanca conglomerate, in which marine fossils occur. Just west of Olean, other fossiliferous marine sandstone beds appear in the lower half of the Cattaraugus redbeds. These units increase in thickness, going westward, until the entire Conewango Stage takes on a marine aspect in the region about Warren, Pennsylvania, and continues so as far


.e, N.Y.
Ithaca, N.Y.-
Chemung, N.Y.
Binghamton,
N.Y.
Wellsburg ss.
Prattsburg ss
orbiculicensis
angusticardinalis
Cayuta ss
chemungensis
Tnt ss
West Hill f
chemungensis
Vertical Scale: 1 inch = 150 feet (approx.)
0 10 20 30 40 50 miles
-partly after Chadwick, 1933

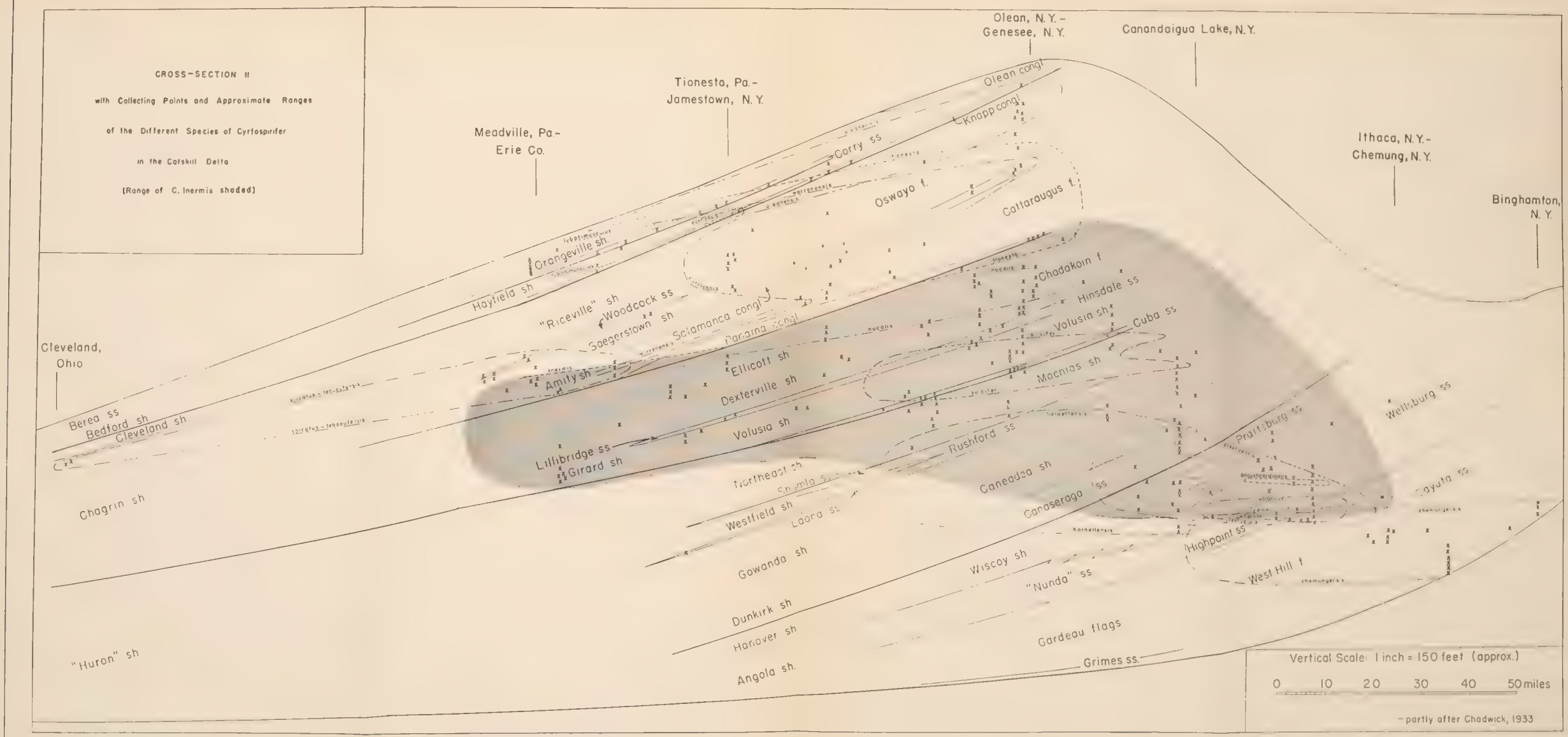


Fig. 4. Cross section of the Middle and Upper Devonian formations from near Binghamton, New York to Cleveland, Ohio, showing collecting points and the approximate distribution of the several species of *Cyrtospirifer*.

west as found. In this marine phase, the Cattaraugus facies is represented by the Amity shale below, the Salamanca formation at the middle, and the Saegerstown shale above, with the Woodcock sandstone above all. The Woodcock is a western development, somewhat restricted in area.

Highest unit of the Conewango Stage is the Oswayo shale. Even in its easternmost facies around Olean, this is a predominantly marine formation, in which fossils are quite abundant. These include a distinctive *Cyrtospirifer*. However, the abundance of shale-chip conglomerates, plant fragments, and mud pellets points to a very near-shore environment of deposition. The base of the Oswayo formation is marked by a thin coquinite over a wide area. In the vicinity of Olean about 100 feet of the upper part of this formation was removed and here it is disconformably overlain by the Knapp conglomerate (Caster, 1934, p. 96).

At the base of the Cussewago Stage (and Mississippian System, according to Caster, 1934), is found the distinctive, and remarkably persistent Knapp conglomerate. It is well-known from Olean, New York, westward as far as Riceville, Pennsylvania. The Tidioute and Hayfield micaceous shales, which make up the rest of the Cussewago Stage, are best known in northwestern Pennsylvania. The Hayfield shale grades upward into the Corry sandstone, of the Berea Stage. This unit is very widespread, and distinctively light gray in color, with an extremely fossiliferous basal sandstone bed.

Above the Corry lies the Cuyahoga Group. "*Spirifer disjunctus*" has been found only in the lowermost formation, the Orangeville shale.

Thus, although largely confined to a particular facies, the tribe of "*Spirifer disjunctus*" persisted through a remarkably long span of time during which widespread deposits of varying composition were laid down.

TAXONOMIC PALEONTOLOGY

HISTORICAL REVIEW OF "*SPIRIFER DISJUNCTUS*"

In 1840, J. de C. Sowerby illustrated the cast of part of a brachial valve of a spiriferid brachiopod which he described thus: "*Spirifera disjuncta.* This, which is a cast of the inside of the upper valve, appears to belong to the species thus named, and is a good illustration of the internal structure of the genus, exhibiting the beak, the muscular impressions, the central striated foramen, and also the hinge area with its striated structure . . . Loc. Barnstaple." (Sowerby, Pl. 53, fig. 8.) In his next plate, the cast of a pedicle valve with a sigmoidal lateral commissure is figured, as well as an exterior view of the same valve. His description of the figures, in part, is as follows: "*Spirifera disjuncta.* Semicircular, with an emarginate front, very convex, radiated; upper valve with about 12 ribs, much raised in the front, forming a rounded elevation; ribs rounded, numerous, about 25 on each side the middle; beaks remote; hinge-area broad, curved, its edges nearly parallel . . . The specimens of this shell are so generally distorted, that its true form is seldom to be clearly made out; and this, added to the difficulty which already exists of determining between the most perfect specimens of different species, renders it very difficult to ascertain to what species they belong. Perhaps even the S. *gigantea* from Tintagel (Pl. LV, figs, 1 to 4) may be distorted individuals of this species.

"Loc. Barnstaple and Petherwin." (*Ibid.*, Pl. 54, figs. 12 and 13.)

On the same plate, Sowerby also figured a very wide brachiopod with many lateral costae, which he described as "*Spirifera extensa.* Fusiform, convex, radiate; about 7 ribs are elevated in the middle of the upper valve; its beak small; radii numerous, commencing along the hinge-line.

"Loc. Barnstaple, Barnstaple Bridge, Saunton, Petherwin."

The internal cast of a brachial valve of a semicircular brachiopod is figured and described as "*Spirifera calcarata.*" "*Spirifera inornata*" and "*Spirifera gigantea,*" the latter apparently large and wide, with numerous radii "proceeding from the hingeline," are obviously greatly crushed and distorted specimens, revealing little of their morphology.

All these forms were lumped together as "*Spirifera disjuncta*" by Davidson (1864), who also figured others of his own as being of this "species."

Meanwhile, Conrad in America had named as "*Delthyris perlatus*" a brachiopod from the Chemung near Blossburg with "hinge margin profoundly elongated; valves with numerous not very prominent ribs; sides flattened, mesial elevation profound" (1841, p. 54).

The following year, a wide form, but one with a wide "mesial fold," he named "*Delthyris chemungensis,*" probably from its having been found at Chemung Narrows, New York.

In 1842, in his report for the Third District of New York, Vanuxem figured a very wide form as "*Delthyris prolata*," and the following year, in his report on the Fourth District, James Hall illustrated as "*Delthyris disjuncta?*" a semicircular form with "short acute ears," which he compares with illustrations of "*Spirifera disjuncta*" by Phillips (Hall, 1843, p. 269). It differs from the latter, he says, in that the mesial fold is not deep, and the ribs are not divaricating or duplicate toward the margin. (It is perhaps worth while to note here that *Cyrtospirifer altiplicus* (n. sp.) from the New York Chemung displays "divarication" in its lateral costae, in many specimens.)

In the same work, Hall figured a wide specimen with many fine ribs as "*Delthyris cuspidata*," but considered it "not improbable that this fossil may be referred to some variety of *Spirifera disjuncta*." Other wide specimens, also from Cayuta Creek, New York, he called "*Delthyris acanthota*," noting the resemblance to *D. cuspidata* and the fact that "they may prove to be varieties of one species." Another figure, described as "*Delthyris inermis*," is not much different from his figure of "*Delthyris disjuncta?*".

De Koninck, meanwhile, included under "*Spirifer verneuili*," as being the oldest name applied to these forms (by Murchison, 1840), the types "*Spirifera gigantea*" and "*S. calcaratus*" of Sowerby and of Phillips (1841).

In his "Palaeontology of New York" (1867), Hall lumped together all the above as "*Spirifera disjuncta*" Sowerby, together with "*Spirifer disjunctus*," so called, apparently for the first time, by Murchison, de Verneuil, and Keyserling (1845, p. 157). Thus included by Hall were also "*Spirifer archiaci*" Murchison (1845, Geol. of Russia, v. 2, Pl. 4, fig. 5), "*Spirifer murchisonianus*" de Koninck (*ibid.*, Pl. 4, fig. 1), "*Spirifer verneuili*" Murchison (1840, p. 252, Pl. 2, fig. 3), and finally even his own *Spirifer whitneyi*.

This seems to be an unfortunate lumping together of unlike elements, for *Spirifer archiaci* is smaller, finer-ribbed, with a pointed beak (more like *S. whitneyi*), while *S. murchisonianus*, according to its figures, is an umbonate, longer, narrower form than anything illustrated by Hall.

Compared with the European species of "*Spirifer disjunctus*," Hall found "no important distinction; indeed the differences in a few individuals are not as great as those among our own specimens recognized as belonging to the same species" (*op. cit.*, p. 245).

In this work of 1867, Hall abandoned his earlier names (*Delthyris cuspidata, D. acanthota, D. inermis*) and was satisfied as to the identity of his species with those given by Sowerby and Phillips under different designations. He therefore adopted the synonymy of Davidson, de Koninck, de Verneuil, Sowerby, and others.

It seems unfortunate that Hall did not make a closer study of his forms at this point, and attempt to delimit their stratigraphic ranges. As will be shown, many of the types are singularly valuable as index fossils to rather well-defined zones in the Upper Devonian and Lower Mississippian of the Appalachian region.

Walcott (1884, p. 134), and Whiteaves (1891, p. 221, Pl. 29, fig. 4) re-

ported "*Spirifer disjunctus*" from the far west: from the Eureka district, Nevada, and from Hay River, Canada, respectively.

In their monograph on the "Palaeontology of New York" (1894), Hall and Clarke gave varietal status to "*Spirifer disjunctus* var. *sulcifer*" a form distinguished by having a sharply defined median sulcus on the fold of the brachial valve.

In China, Grabau redefined many forms of "*Spirifer disjunctus*," placing most emphasis on "the nature and mode of appearance of the sinal plications of the pedicle valve" (1931a, p. 209), and united them under the subgeneric name of *Sinospirifer*. *Spirifer lonsdalii*, *S. verneuili*, *S. disjunctus*, and *S. whitneyi* were retained as distinct species, however, the last two being grouped as "American relatives of the group to which *S. sinensis* [the type for his subgenus *Sinospirifer*] belongs." He further considered *Spirifer whitneyi* as "clearly an American mutation of the Chinese form, while *S. disjunctus* "may be an immigrant from Europe," since "a part at least of the Chemung fauna of New York etc. may be of Atlantic origin" (p. 346–347).

Spirifer archiaci Murchison seems to have been absorbed into Grabau's morphological series of sinospirifers.

After definition of the genus *Cyrtospirifer* by Nalivkin (*in* Fredericks, 1926), the "species" *Spirifer disjunctus* has been included within its ranks (Cooper, 1944).

Finally it should be noted that in Europe and elsewhere some paleontologists consider *Spirifer verneuili* and *S. disjunctus* to be one and the same, while others consider them separate entities, with supporters on both sides as to the priority of the specific names "*disjunctus*" and "*verneuili*" (e.g., Gosselet, 1880).

From the above review, it is apparent that the brachiopod group of which the Appalachian cyrtospirifers form a part are in a confused state of taxonomy. The present work attempts to clarify a provincial spiriferid tribe which represents only part of a world-wide group; one which burgeoned greatly during its span of geologic time. Only tentative attempts to relate the North American forms of "*Spirifer disjunctus*" with those found in Europe and Asia have been essayed. Lack of availability of good types from those regions, and (for the most part) unreliable figures and descriptions in the early works cited make this necessary.

SYSTEMATIC DESCRIPTIONS

Phylum Brachiopoda
Superfamily Spiriferacea Waagen
Family Spiriferidae King
Genus *Cyrtospirifer* Nalivkin, *in* Fredericks, 1926

The first published description of the genus *Cyrtospirifer* was that of Fredericks (1926), citing an unpublished manuscript by Nalivkin bearing the date 1918. (Fredericks, 1919, made use of the generic name earlier, but did not describe the genus.) It is clear from the contents of Fredericks' publication of 1926 that Nalivkin was responsible for the name and its definition.

Fredericks' description of the genus is most inadequate, as he was more anxious to fit it into the proper pigeon-hole in his taxonomic grid, which was based on a few shell features, than to adequately describe the generic characteristics. He included it in his Subfamily VIII, Cyrtiinae, which embraced spirifers with an "ostiolate apical apparatus; apical lamellae, and a delthyrial lamella." On his grid, which was based on the surface features and texture of the shell only—a quite arbitrary and exclusive system—*Cyrtospirifer* was further described as having a glabrate shell texture and costate surface.

The important characteristics possessed by the genus and stressed by Fredericks are dental lamellae (his "apical lamellae"), and a "delthyrial lamella" (i.e., delthyrial plate). In an English translation of his own paper,* Fredericks says, "This type of structure of the apical apparatus is distinctly characteristic of the development between the bases of the apical plates of a delthyrial plate, which is not to be confounded with the deltidial ones which represent in the brachiopods a primary element of the shell." That is, a flat or concave delthyrial plate is present in the genus, but not an outward-curving deltidium. Fredericks continued, "As is known, the delthyrial plate is subject to two modifications, viz: the simple one and that with wings. In the last case it is followed by a development of the so-called 'apical callosity.'"

A much better description of his genus was given by Nalivkin in 1930 (p. 196–197). He says that Peetz (1901, Beiträge zur Kenntniss der Fauna aus den devonischen Schichten, am Rande des Steinkohlen bassins von Kuznetz: Travaux Sect. geol. Cab. S.M. St. Petersburg, IV) "explored the internal structure of Central Russian specimens from the group of *Spirifer Verneuili* and pointed out that, owing to the presence of a delthyrial plate—'rostral callosity,' it corresponds to that of the group *Osteolati* Hall et Clarke. Yet their reference to this group is prevented by the presence of a plicated sinus and mesial elevation. According to Hall and Clarke, the group *Osteolati* is characterized by a smooth sinus and mesial elevation."

"The group of *Spirifer Verneuili*," he goes on, "can equally not be ranged under any of the subdivisions proposed by Schuchert (Zittel, Textbook of Paleontology, 1913, p. 410)."

All this, Nalivkin says, compelled him to separate "all the species allied to *Spirifer Verneuili* into a special subgenus *Cyrtospirifer* nov. subgen."

After describing some very general shell features of the genus, Nalivkin says: "The ventral valve bears two more or less developed dental plates. In the apical region, near the area, these plates are connected by a delthyrial plate ("rostral callosity"). This latter is present in all the specimens, independently of the height of the area and of their age.

"Genotype: *Spirifer Verneuili* Murchison."

These forms are to be distinguished from their nearest allies, subgenus *Theodossia* Nalivkin, "by the absence," in the latter, "of a delthyrial plate (rostral callosity), flatter and densely set plications, a faintly developed area, whose length is inferior to that of the hinge margin and by feebly developed sinus and mesial elevation."

After remarking on the exceedingly wide geographic distribution of the subgenus, Nalivkin says: "Their vertical range is more restricted. Appearing in the upper horizons of the Mesodevonian, the subgenus *Cyrtospirifer* attains its

* Manuscript translation in English of Fredericks (1926), by its author, sent to Dr. Schuchert, and now in the Yale Peabody Museum Library.

maximal development in the lower horizons of the Neodevonian and dies out in the transitional deposits between the Devonian and Carboniferous."

From these two accounts, it appears that one of the most truly diagnostic features of *Cyrtospirifer* besides the shape of the shell, ostiolate apical apparatus, and bifurcating costae of the sinus and fold with simple lateral costae, is the possession of a "rostral callosity," or delthyrial plate, connecting the dental lamellae in the apical region. All the forms of "*Spirifer disjunctus*" presently to be described possess this feature in greater or lesser development. They also have the other, more general, and in some ways less distinctive characteristics of the genus.

Grabau recognized a "morphological series" among the Spiriferidae of China to which he gave subgeneric rank, and the name *Sinospirifer* (1931a). He thought that the European group of *Spirifer verneuili*, "commonly regarded as synonymous with *Spirifer disjunctus* Sowerby," constituted "an independent morphological series, probably paralleling many of the Chinese forms, but developed within its own restricted habitat" (p. 208). But that the two series were closely related Grabau said "can hardly be questioned." In the few types he studied (including one of Hall's type specimens of "*Spirifer disjunctus*" from Cayuta Creek, New York), Grabau said that "the order of development of the morphological characters is the same as for the Chinese form, but the rate of development varies, i.e., there is differential acceleration and retardation in development of the European series which is distinct from that of the Chinese series. Nevertheless, . . . there are certain forms which correspond so closely in the two series, that they are practically inseparable."

The question raised here is whether or not any of the forms of "*Spirifer disjunctus*" from the American Appalachian province belong to the subgenus *Sinospirifer*.

Grabau lists as the most important morphic (*sic*) structures the nature and mode of appearance of the sinal plications of the pedicle valve. Next to this the shell index (i.e., the ratio of shell width to length) was considered of major importance. One characteristic stamping the greatly variable Chinese forms as a morphologic group distinct from the European and American forms, Grabau states, is the smaller size, scarcely ever exceeding one-half the dimensions of the typical British *Spirifer disjunctus*. The Chinese forms, according to Grabau, also have a fine radial striation, which is present as well in the Western American *Spirifer orestes* and *S. whitneyi*. These two spirifers, therefore, are considered to be derivatives of the Chinese rather than of the European and eastern American forms of *S. disjunctus*. This last characteristic may have a pertinence in the evolution of the species of the Appalachian province which will be discussed in its proper place.

Grabau never gave an adequate description of the general morphology of his subgenus *Sinospirifer*. Nowhere did he pay much heed to the internal structures. To him, the manner and the order of bifurcation of the costae of the sinus, and the shell index were all-important. Since the brachiopods of the present study fit very well into Nalivkin's genus *Cyrtospirifer* but not at all well into the poorly defined and confusing subgenus *Sinospirifer*, they have been recognized as belonging to the genus *Cyrtospirifer*.

On the basis of the first of these features—bifurcation of the costae—three divisions of spirifers were erected (Grabau, 1931b):

1. Uniplicate Division, characterized by a single ("primary") median plica in the sinus, which may remain simple, or bifurcate once, or several times. It is the

dominant group in the Middle Devonian. Genera: certain species of *Schizospirifer, Plectospirifer, Indospirifer, Centrospirifer.*

2. Triplicate Division, in which two primary sinal plications begin, "which branch from the bounding plications a short distance below the beak and gradually diverge forward, so as to divide the sinus into three more or less equal portions, a median and two lateral. In the lateral portions, the further development of plications proceeds according to a definite rule. The first pair of laterals branch off from the bounding plications in the same manner as the primary plicae, and usually there is a second pair branching off still further forward, and often a third pair. The primary plicae remain simple or bifurcate, and the lateral plications likewise may bifurcate, though the last or outermost of these, which is also the shortest, usually remain simple. Again intercalated plicae may appear, either between the primary and first pair of laterals, or between the laterals themselves.

"The median system develops independently from the lateral system and the first pair of median plicae is always parallel, or nearly so, to the primary plications. It arises independently inside of the primary pair. A second pair is generally formed, this appearing later and inside of the first pair, i.e. nearer to the center of the sinus." A third, and more rarely a fourth pair may appear, successively towards the center. There may or may not be a single central plication but this commonly appears after the first pair of medians, or even after the later pair. The central plicae, as well as some or all of the median plicae, may remain simple or divide once or several times.

Range as known to Grabau: neither below nor above Upper Devonian.

Species: *Sinospirifer subextensus* (Martelli), S. *subarchiaci* (Martelli), S. *pellizzarii* Grabau; here too are listed "*Sinospirifer whitneyi* Hall," and "*Sinospirifer disjunctus* (Sowerby) Hall."

3. Dupliplicate Division, in which two primary plicae appear, but instead of diverging, remain essentially parallel, and paired plicae are developed only in the lateral portions. Lateral shell plications show "frequent bifurcation" as well. Confined essentially to the Carboniferous and Permian.

Genera: species of *Platyspirifer, Choristites, Spirifer, Spiriferella, Brachythyrina.*

Since the costae of the sinus in all the cyrtospirifers from the Appalachian province bifurcate according to the rules set down by Grabau for his Triplicate Division, those forms may possibly be included therein.

Grabau did not attempt to define the relationship of Nalivkin's genus *Cyrtospirifer* to his grouping, although he was aware of the definition of the genus.

Gatinaud (1949) gave a good resumé of the method and development of the system using sinal plications and formulae. The diagrams and formulae of Grabau, he says, will serve only to distinguish between species of the same genus or subgenus, or between morphologic groups comprising several genera or subgenera, but not the genera or subgenera themselves (p. 153). For the latter purpose, closer scrutiny of the order of appearance of the sinal plications and their bifurcations he considers necessary. The plications of the shell are said to be a result of the organization of the mantle, which evolves parallel to the internal calcareous structures, hence is considered to be of prime importance. This is open to question, it seems to me, for the generally prominent costae on the sides of a spirifer certainly do not follow the evolutions of the spiralia—the only known internal calcareous structure in that part of the shell (cf. Caster, 1930, Pl. 5 (26), fig. 1). What conceivable internal structures in the section of the shell beneath the sinus exist that should be of such fundamental importance in the shell's development, and that

should be reflected on the sinus? Gatinaud does not say, nor does the literature on spirifer morphology mention any such structures.

Starting with sinal formulae developed for the Dalmanellacea by Bancroft (1945, Jour. Paleontology, v. 19, p. 181–252), Gatinaud's method goes much further in their use. The total number and stage of appearance of the costae and their bifurcations in the two lateral sectors and the median sector of the sinus in the Spiriferidae are compared and contrasted. These comparisons are made possible by an ingenious method of grades, indices, counter-indices, modules, quotients, perquotients, logarithmic indices and logarithmic quotients, designed to bring out otherwise-hidden differences in the costation of the sinus in the different genera. Almost solely on this basis, a new systematics for the group is erected. In this scheme, *Cyrtospirifer* Nalivkin, with its genotype *Spirifer verneuili* Murchison (1840), is given generic rank, and included among its 3 new subgenera is *Eurytatospirifer*, of which *Spirifer disjunctus* Sowerby (1840) is the genotype.

It may be that the method of Gatinaud and Grabau in which overwhelming importance is attached to one shell character for taxonomic classification is justified. On the other hand, neglect of such features as internal structures and microornamentation, which have proved so valuable in other brachiopod families, hardly seems warranted for the spirifers. It is not presumed that the costae of the sinus may not be of great importance; in the *Cyrtospirifer* clan of eastern North America there appears to be some harmony with Grabau's Triplicate Division. Undoubtedly in this group two initial primary costae do appear, creating a threefold division of the sinus. But the disadvantages in the use of one feature alone in erecting taxonomic plans are self-evident: we become blind to other shell characteristics which may be of equal, or even greater, systematic significance; the use of Grabau's and Gatinaud's method requires the most perfect shell preservation in the early stages of shell development, and exactly in those parts of the shell where erosive processes are most active; what may be only individual variation within one shell feature (the costae of the sinus) may be magnified out of all proportion to its true taxonomic value.

All the American species of "*Spirifer disjunctus*" studied possess morphologic features diagnostic of *Cyrtospirifer* Nalivkin; they have therefore been included in that genus. Early features of the sinus, which are so important in diagnosing Grabau's and Gatinaud's groups, are not well preserved in species from the Appalachian province. However, because the order of appearance and bifurcation of the costae of the sinus may eventually become critically valuable, these features have been described as accurately as possible, and, quite often, a plate figure to illustrate has been presented as well.

Only a greatly prolonged study of the entire group will finally decide the true relationships of the spirifer complex. The present work is offered as a small contribution to that end.

Cyrtospirifer chemungensis (Conrad, 1842)

Plate 1, figures 1 to 8; Pl. 3, figures 1 to 6.

Delthyris chemungensis Conrad, 1842, p. 263.
[?] *Delthyris prolata* Vanuxem, 1842, p. 179, fig. 3, and p. 181.
Delthyris cuspidata Hall, 1843, p. 270, fig. 1.
Delthyris acanthota Hall, 1843, *loc. cit.*, fig. 2.
Spirifera disjuncta Hall, 1867, [non Sowerby], p. 247, figs. 1 to 3, p. 41, fig. 19.
Cyrtospirifer disjunctus (Hall) Cooper, 1944, p. 321, Pl. 122, figs. 1 to 3.

DESCRIPTION. Shell very wide, with mucronate extremities, and of a form well shown in Plate 1, figures 1 to 8.

Pedicle valve evenly and gently arched from beak to front. Transverse arching greatest next to the sinus, where it is sub-acute, thence gently concave outwards to extremities, making a distinctive transverse profile (Pl. 1, fig. 5). Sulcus shallow, not especially broad, starting at the beak, and well-defined. Umbo small, only slightly projecting beyond the hingeline, and slightly incurved. Cardinal area curved, vertically finely striate, narrowing evenly toward extremities. Delthyrium about as broad as high, with narrow delthyrial flanges. No deltidial plates are observable in the specimens available. Dental lamellae restricted to the beak area only, divergent, and continued forward as low, slender, converging ridges, which unite to enclose the muscle scar. The latter small, subcordate, longitudinally striate, and, in old individuals, deeply embedded. Teeth short, low.

Brachial valve convex, to a similar degree as that of the pedicle valve. Fold arising at the beak, gently rounded, fairly well-defined at the sides. Transverse arching greatest next to the fold, commonly slightly depressed at about one-third the distance to the extremities. Umbo small, only slightly projecting. Dorsal cardinal area narrow, and extending out to the extremities. Socket plates stout.

Exterior of both valves covered with numerous, round-topped costae, simple on the lateral slopes, bifurcating on the fold and sulcus. Those on the sides number 50 or more on each side, and the majority of them begin at the hingeline, rather than on the umbo. About the first 10 costae on each side nearest the midline arise on the umbo, however. Bifurcation of the costae of the sinus begins either with the median costa or with the admedian pair. It may also take place in the two initial, primary costae somewhat later. Thus there appears to be considerable variation in this respect. At a distance of 1.5 cm. from the beak, there are an average of 10 costae present, in the sinus. Fine growth lines are present as micro-ornament.

DISCUSSION. This species is distinguished by its great width, its mucronate extremities, its small, subcordate muscle scar partly enclosed by the restricted dental lamellae, and by its numerous fine lateral costae arising from the hingeline. The subangular arching of the shell lateral to the sinus makes a very distinctive transverse profile. *Cyrtospirifer vandermarkensis* n. sp. (p. 27) possesses many of these features, but lacks the fine mucronate extremities, and has a much higher cardinal area. Considerable variation in size, mucronation, costation, etc. is shown by this species in the upper limit of its range (Pl. 3, figs. 1 to 6).

The earliest descriptions of fossils which may belong to this species are those of Sowerby (1840, Pl. 53, fig. 9, and Pl. 54, fig. 11), originally named *Spirifera inornata* and *Spirifera extensa*, and obtained from localities in England. However, as he states that his material was much crushed and distorted, he was unable to give adequate descriptions or figures of the types. For this reason it is felt that the best interests of taxonomy will be served if his species are no longer considered recognizable.

This is the form described by Conrad in 1842 under the name *Delthyris chemungensis*. His types were from Chemung Narrows, New York. Although he did not illustrate the species, his description combined with the collecting locality leave no reasonable doubt that this is the form he named.

C. H. Crickmay (1952a) described and figured a wide spiriferid shell, somewhat similar to this, obtained from the Hay River shale. This *Cyrtospirifer glaucus* (Crickmay) he later made the genotype of a new genus *Regelia* (1952b) on the

basis of "its exaggeratedly transverse shell-outline, and (early species at least) lack of micro-ornament." But many species of *Cyrtospirifer* exhibit great variation in width of shell, a feature which need not justify erection of a new genus; nor is the presence of micro-ornament diagnostic of the genus *Cyrtospirifer*. It has, therefore, been thought best to classify the New York form under *Cyrtospirifer*.

C. chemungensis differs from the Hay River species only in its distinctive transverse profile, and perhaps finer costation. If not equivalent, the two forms at least are closely allied both morphologically and chronologically. Conrad's specific name has priority over that of Crickmay.

Considerable variation in size, mucronation, costation, etc. is shown by this species in the upper limit of its range (Pl. 3, figs. 1 to 6).

Distribution. This is the earliest form of "*Spirifer disjunctus*" to be found in the New York Upper Devonian. It has a fairly restricted stratigraphic range, being limited to about the lower half of the Cayuta formation. Excellent exposures containing an abundance of *Cyrtospirifer chemungensis*, but apparently no other forms of the tribe, are to be found along the highway about one mile north of Owego, New York. The highest occurrence of this species is some 300 feet above the base of the Chemung in the vicinity of Elmira, New York, where, however, a considerable variety of congeneric forms are to be found as well.

Cyrtospirifer altiplicus n. sp.

Plate 1, figures 9 to 12; Plate 2, figures 1 to 5.

Delthyris perlatus Conrad, 1841, p. 54.
Spirifera disjuncta Hall, 1867, [non Sowerby], Pl. 42, fig. 20, Pl. 41, fig. 17(?).

Description. Shell large, wide, very mucronate. Pedicle valve moderately and evenly arched from the beak. Transverse profile convex near the sinus, becoming gently concave about one-third the distance to the extremities. Sulcus shallow, rounded, very wide, well-defined. Umbo projecting broadly beyond the hingeline. Cardinal area high, wide, vertically finely striate, and gently curved, with narrow delthyrial flanges. Dental lamellae divergent, and extending forward into the shell for about one-third its length. Delthyrium about as wide as high, and closed for about the upper one-third by secondary growth from the sides, and, especially, from the floor of the beak region. Teeth narrow, wide, and curved.

Brachial valve convex, and arched to a somewhat similar degree as the pedicle valve. Fold high, narrow, rounded, distinctive, and well-defined right to the beak. Umbo broadly projecting beyond the hingeline. Dorsal cardinal area rather high, extending out to the extremities, as shown in Pl. 2, figure 5. It is also gently curved, and vertically striate. Tooth sockets narrow, wide, and curved, with stout crural plates.

Exterior of both valves covered with numerous round-topped costae, bifurcating greatly in sinus and on fold, but simple on the lateral slopes. However, the costae on the sides show a distinct tendency, on some specimens, toward bifurcation, or even trifurcation, toward their front ends. In the sinus of the figured specimen, Plate 2, figure 2, two primary costae arise initially, then two more just inside these. Next, a median costa appears, which divides almost at once. The left branch of this division bifurcates rapidly; the right branch only near the front of the shell. New costae come in from the sides of the sinus, and the primary costae divide at about two-thirds of the shell length.

The first 24 or so of the lateral costae arise in the umbonal region, while the

later ones have their origin at the hingeline. The total number may be 50 or more, on each side. Fine growth lines are present as micro-ornament.

The name adopted for this species is derived from the elevated fold, which is so distinctive a feature of the form.

Discussion. The size and shape, mucronate extremities, divergent dental lamellae, and numerous fine costae, many beginning at the hingeline, are distinctive for the species. Also particularly diagnostic, and serving to distinguish *Cyrtospirifer altiplicus* from *C. chemungensis* (Conrad), are its wide, shallow sulcus, and very high, rounded, narrow fold. The dental lamellae are more extended and the hingeplate in the brachial valve larger and stronger than in *Cyrtospirifer chemungensis*. Also distinctive is the tendency toward tripartition in the lateral costae, and the more numerous bifurcation of ribs on the sinus and fold. *Cyrtospirifer vandermarkensis* (n. sp.) lacks the distinctive high fold and broad sulcus, as well as the mucronate extremities of the species here considered.

Distribution. This species occupies a restricted zone in the Cayuta formation and its equivalents, just above that of *Cyrtospirifer chemungensis*. The two forms have not been found together, and furthermore, although *Cyrtospirifer altiplicus* follows just after *C. chemungensis*, strata above the latter in the area of the type Chemung are largely depleted of fossils—including *Cyrtospirifer altiplicus*—due perhaps to environmental control at the time of deposition of the beds. There is also a limited zone intermediate to the two types in which a considerable variety of odd forms probably of the species *C. chemungensis* are found.

Cyrtospirifer altiplicus ranges upward in the "Cayuta" formation through a thickness of strata not much greater than 100 feet. It is limited in its lateral distribution as well, due probably to strict facies control. For, despite the coeval existence of *Cyrtospirifer hornellensis* (n. sp.), the latter predominates in the shaly, presumably farther offshore, facies of the Wiscoy formation and its equivalent beds. *Cyrtospirifer altiplicus*, on the other hand, is found most abundantly in the near-shore sandstone facies.

The best specimens of this species were found opposite the railroad station at Sabinsville, Pennsylvania (by E. I. Leith), and in sandstone outcropping in a stream bed one-half mile south of that town. Excellent exposures with abundant fossils may be found in Ryers Creek, 3 miles northeast of Lindley, New York.

Cyrtospirifer angusticardinalis n. sp.

Plate 2, figures 6 to 13.

Description. Shell subtrigonal in shape, with hingeline equal to, or less than, the greatest shell width.

Pedicle valve most convex near the beak. Lateral slopes evenly convex. Sulcus beginning at the beak, shallow, rounded, or slightly V-shaped, in some, and fairly well-defined. Umbo projecting well beyond the hingeline. Cardinal area very high, narrowing abruptly toward extremities, and only slightly curved. Delthyrium higher than wide; more than one-half of its upper portion may be closed by a callus of secondary growth from the inside floor of the shell. The dental lamellae extend forward for one-half to two-thirds the shell length, and are moderately divergent, following the margins of the sinus rather closely. Muscle scar not well known, but apparently confined within the dental lamellae for most of its length.

Brachial valve markedly convex, with well-defined fold beginning at the beak,

fairly high and rounded, and widening somewhat toward the front. Umbo broadly projecting beyond the hingeline.

Exterior of both valves covered with rather fine, rounded costae, which bifurcate only on the fold and sulcus. On the latter two parts of the shell, bifurcation begins earlier and occurs more often than in most other forms of the "*disjunctus*" tribe studied. Hence, at any place on the fold or sulcus, rather numerous costae are to be found. In the sinus, two primary costae arise at first, followed almost immediately by two more just inside these. The latter bifurcate very soon thereafter; two more appear inside these, and proceed to bifurcate. New costae arise from the inside of the two costae bounding the sinus, and, on the specimens studied, the two primary costae themselves bifurcate at one-half, or more, of their length. By far the greatest amount of bifurcation takes place in the costae nearest the midline. No micro-ornamentation, other than fine growth lines, has been observed.

Discussion. The distinctive shape of shell, high cardinal area, rather short hingeline, and finer costae, which bifurcate greatly on the sinus and fold, distinguish this species from anything found in its zone of the Chemung. Just below it in the section, the utterly different, wide shells of *Cyrtospirifer altiplicus* are found. *Cyrtospirifer inermis* (Hall) appears a little later, and is easily distinguished from the present species by its wider shell with angular extremities, coarser ribs, which also bifurcate less, lower cardinal area, and shorter dental lamellae. The latter structures also commonly diverge more than do those in the present species.

Distribution. First found in Cayuta sandstone, just below the presumed base of the Wiscoy formation, in the vicinity of Corning, New York, this species has also been found ranging upward to near the top of the Wiscoy formation, also in sandstone, across the border into Pennsylvania. Thus, it would seem to have a restricted range. Its abrupt appearance, with apparently no forms intermediate to other species, may indicate that we are here dealing with an exotic migrant.

Cyrtospirifer preshoensis n. sp.

Plate 3, figures 7 to 16.

Description. Shell medium-sized, distinctively subquadrate in outline, as shown in Plate 3, figures 7 and 12. Some, however, attain a larger size and more triangular shape (fig. 15).

Pedicle valve greatly arched, and obese. Lateral slopes moderately convex. Sulcus broad and deep, fairly well-defined to the beak. Umbo sharp, incurved, and projecting well beyond the hingeline. Cardinal area high, curved, triangular, and vertically finely striate. Delthyrium higher than broad, and open almost to the apex in all specimens examined. Closure is done mainly by a small amount of secondary growth, apparently. Dental lamellae extend well into the body of the shell, following the margins of the sinus rather closely for most of their length, but in some specimens these become subparallel for about the last one-third of their length. The lamellae reach at least half the distance to the front of the shell; generally their extent is greater than that. Muscle scar enclosed for its posterior part by the dental lamellae. Teeth long, slender, and slanted outward toward the beak.

Brachial valve convex, although much less arched than the pedicle valve. Fold high, rounded, and prominent to the beak. Umbo broadly rounded, and pro-

jecting beyond the hingeline. Dorsal cardinal area rather wide in the region of the beak, narrowing toward the shoulders, and vertically striate. Dental sockets long and slender, following the outward trend of the beak. Crural plates prominent, distinctively shaped, as shown in Plate 3, figure 8.

Exterior covered with fairly broad, rounded costae, simple on the lateral slopes, but bifurcating greatly on the fold and sinus. In the sinus, two primary costae arise initially, and remain simple, in the specimens studied, the full length of the sulcus. Inside these, new costae appear, bifurcate, then their branches bifurcate repeatedly so that rather numerous, finer ribs are seen between the rather more prominent, simple costae of the sinus. Only one or two new costae arise from the sides of the sinus.

A distinctive micro-ornamentation is present. This consists of fine, imbricating, flattened spicules across the tops of the costae, with fine liration in the grooves between the costae. The latter, however, probably represent the unworn, longer, hair-like spicules which are partly eroded on the tops of the costae. There are about 3 or 4 of these spicules on the tops of the ribs, while they number about 7 or 8 per millimeter along the length of a costa. (Pl. 3, fig. 16.)

Discussion. This species may be distinguished from *Cyrtospirifer inermis* (Hall), which it may superficially resemble, in its commonly more quadrate outline, greatly arched pedicle valve, and more convex brachial valve, broad sulcus with complementary high, rounded fold, much longer dental lamellae, more open delthyrium, distinctively shaped crural plates, and finely spinose micro-ornamentation. Most of these morphologic features, as well as the coarser costae, also serve to differentiate it from *C. angusticardinalis.*

The subquadrate shape and medium size of the average specimen of this species, together with its greatly arched pedicle valve, and long, moderately divergent dental lamellae—quite unlike any other forms of "*Spirifer disjunctus*" at its zone in the Upper Devonian—are suggestive of the genus *Cyrtiopsis* (Grabau). The outward form especially resembles illustrations of *Cyrtiopsis kayseri* (Grabau, 1931a, Pl. 46, figs. 6-9). However, in his discussion of the morphology of *Cyrtiopsis*, Grabau notes a "well-developed pseudo-deltidium marked with a foraman near its apex," and "fine radial striation especially well-marked in the sinus" (*op. cit.*, p. 422–423). These features are lacking in the individuals described here. It is concluded, therefore, that these forms belong to to the genus *Cyrtospirifer,* although, in view of their sudden appearance in the midst of types of altogether different aspect, it is considered possible that these represent exotic forms not endemic to the New York Chemung province.

There is a striking superficial similarity of this species to *Spirifer archiaci* Murchison as described in "Geology of Russia, Part II" (1845), and especially Plate 4, figures 5 (f) and (g). The same high area, relatively narrow shoulders, and sharp beak are present. More significantly perhaps, the finely spinose micro-ornamentation, which is so distinctive a feature of *C. preshoensis*, is also illustrated in the same plate (fig. 5 e). *S. archiaci* has been collected from Upper Devonian beds on the banks of the Don, near Zadonsk, and at Octrada, in Russia, and in beds of "comparable age" in Belgium (*op. cit.*, p. 156).

Distribution. This species first appears in the upper part of the Cayuta formation, just above the zone of *C. chemungensis*, and below that of *C. altiplicus.* It is in this limited thickness of strata that a great variety of individuals of the "*disjunctus*" tribe is to be found. Most of these are tentatively considered to be variants of *C. chemungensis; C. preshoensis,* however, with its greater strati-

graphic range and more distinctive morphology is thought to be worthy of specific rank. The first specimens were collected along Glendening Creek, at Presho, New York, and from that town the specific name has been derived.

A great decrease in numbers of *Cyrtospirifer preshoensis* takes place throughout the remaining thickness of the "Cayuta" and most of the Wiscoy formation. In the upper part of the Wiscoy, and the lower part of the Canaseraga sandstone, another "flood" of *C. preshoensis* appears. The main body of the Canaseraga sandstone is deficient in all forms of "*disjunctus*." The highest occurrence of *C. preshoensis* certainly identified was higher still, in thin sandstone beds at the base of the Caneadea formation.

This species was invariably found in sandstone beds, either in layers a few inches thick, or as lenses. In their typical occurrences at Ryers Creek, and near Addison, New York, in the equivalent of the upper part of the Cayuta formation, they are found in intimate relationship with "storm rollers" and redbeds. It seems quite possible, therefore, that we are here dealing with a form which dwelt very near to the shore.

Cyrtospirifer inermis (Hall)

Plate 4, figures 1 to 16; Plate 10, figure 4

Delthyris disjuncta ? Hall, 1843, [non Sowerby], p. 269, fig. 3.
Delthyris inermis Hall, 1843, *op. cit.*, p. 270, fig. 4.
Delthyris cuspidata Rogers, 1858, p. 829, fig. 683.
Spirifera disjuncta Hall, 1867, [non Sowerby], p. 243, figs. 4 and 5, Pl. 41, figs. 1–3 and 5–9; Pl. 42, figs. 6(?), 7, 8, 9, 10(?), 11, 12, 14, 15, 16, 17(?), 18(?).
[?] *Spirifera disjuncta* Whiteaves, 1891, [non Sowerby], p. 221, Pl. 29, fig. 4.
Spirifer disjunctus Hall and Clarke, 1894, [non Sowerby], Pl. 30, fig. 15.
Spirifer disjunctus Hall, [non Sowerby], Caster, 1930, Pl. 2 (23), fig. 2; Pl. 3 (24), fig. 6(?).

Description. Shell of medium to large size, subquadrate, with angular or mucronate extremities, and sigmoidal lateral commissure. This species shows considerable variation in size. The average is about 50 mm. wide, and 30 mm. long. However, some large individuals measure over 80 mm. in width, and 45 mm. in length.

Pedicle valve with greatest arching toward the beak. Lateral slopes evenly convex, or else with slight depressions about two-thirds the distance to the extremities. Sinus shallow, rounded, fairly well-defined from the beak. Delthyrium generally about as wide as high, closed for its upper one-third, or so, by secondary calcitic growth from the base of the dental lamellae and the floor of the beak region. Dental lamellae divergent, and commonly extending forward into the shell for about one-third its length, but these structures show considerable variation in both length and divergence. A spear-shaped "apical callus" extends forward from the juncture of the lamellae into the muscle area, making the latter bifid behind. The entire umbonal region becomes heavily callused with secondary growth. Muscle scar ovate, expanded and round toward the front, longitudinally striate, and partly enclosed by dental lamellae. Teeth rather slender and elongate.

Brachial valve convex, less arched than pedicle valve. Fold extending to the beak, rounded, of moderate height, and well-defined. Tooth sockets long, narrow, and small. Crural plates stout. Dorsal muscle scar never prominent. A low, slender median ridge follows along the inside of the fold for about one-third its length. Dorsal cardinal area narrow, and extending to the extremities.

Surface of both valves covered with round-topped costae, simple on the lateral slopes, but bifurcating on the fold and sulcus. The average number of costae on

each side is about 24, all beginning in the umbonal region. Large and wide specimens may have more lateral costae, but these never exceed about 36. Costae in the sinus bifurcate most commonly in those members nearest to the midline, but new costae also arise as off-shoots from the lateral plicae which bound the sinus. It is not uncommon for one costa just to one side of the midline to bifurcate more frequently than any of the others, thus introducing an asymmetrical element into an otherwise symmetrical shell.

Considerable variation exists in the mode of bifurcation in the sinus (Pl. 4, fig 1. and 2). A very common method is as follows: Two primary costae appear initially, remaining simple for their entire length. Next in appearance is a median costa, which splits into two almost at once. The next to bifurcate is one or both of the off-shoots of this initial bifurcation. Next, at the sides of the sulcus, two new costae appear, and, nearer the front of the shell, other new members arise from this border, as well. Bifurcation in the sinus divisions lateral to the two primary costae is less common than in the median area between them. In some shells, a new median costa may arise by intercalation and it too may bifurcate, as it proceeds forward.

Only fine growth lines are present as micro-ornament.

Discussion. The umbonate character, more extended dental lamellae, fewer lateral costae which begin in the umbonal region, and much less extended hingeline distinguish this species from *Cyrtospirifer chemungensis* and *C. altiplicus*. The shape of the shell, less prominent fold, longer dental lamellae, and lack of tendency toward tripartition in the lateral plicae are distinctive features, contrasting this species with *C. altiplicus* in particular. The larger size, different shape, lack of spinose ornamentation, and umbonate nature differentiate this species from *Cyrtospirifer hornellensis* (n. sp.). It does not have the broad, flat ribs covered with fine growth lines, wide, gently rounded, ill-defined sinus, nor radiately striate muscle scar with more prominent adductor scar, of *Cyrtospirifer tionesta* (n. sp.). The brachial muscle scar is much less prominent, and the hingeplate much narrower than in *Cyrtospirifer oleanensis* (n. sp.). *Cyrospirifer sulcifer* (Hall) has a prominent median groove on its fold, which is lacking in this species.

Considerable variation takes place in *Cyrtospirifer inermis*, both within a bed and throughout its stratigraphic range. In the great majority of cases, this is probably individual variation within a single species, commonly an adaptation to a new environment of local nature and relatively limited duration. The large, coarse-ribbed individuals shown in Plate 4, figure 16, and Plate 10, figure 4 are from the thick sandstone beds of the upper part of the Canaseraga formation, and possibly reflect in their morphology an adaptation to the near-shore, strong wave-action presumed for their sedimentary environment. Both specimens are from the same bed, hence were about co-existent, yet one has developed a much wider shell than the other. Similar, although less striking, instances are known from other parts of the stratigraphic section.

In at least two other cases, however, the change in morphology is so great, and the stratigraphic range so well-delimited, that the erection of new taxonomic groups is thought to be justified. These are *Cyrtospirifer sulcifer* (Hall) and *C. nucalis* (n. sp.).

Cyrtospirifer inermis is one of the most common fossils found in the Upper Devonian of New York and Pennsylvania. It is the widest-ranging, both stratigraphically and geographically. Hence, it is not impossible that this spirifer, or

forms closely allied to it, existed coevally in other regions of the world as well. Sowerby, for instance, in the earliest description of shells of this type, illustrated something similar (1840, Pl. 53, figs. 7 and 8; Pl. 54, figs. 12 and 13), as did Phillips (1841, Pl. 29, figs. 127, 128z and γ; Pl. 30, fig. 129), and Davidson (1864, Pl. 5, figs. 3–12; Pl. 6, figs. 1–3 and 5–8). Whiteaves described and illustrated as "*Spirifera disjuncta*" a similar spiriferid shell from Hay River, in western Canada (1891, p. 221, Pl. 29, fig. 4). Furthermore, many of Grabau's Chinese sinospirifers superficially resemble *Cyrtospirifer inermis* (1931a, p. 231 ff., Pl. 28 *et seq.*). It is somewhat unfortunate that lack of opportunity for a closer study of foreign forms of "*Spirifer disjunctus*" prohibits anything but the most tentative correlations.

Since the species here described seems to be identical with forms first described and illustrated by James Hall as "*Spirifer inermis*," it is felt that the best interests of taxonomy will be served by reviving Hall's specific name.

Distribution. *Cyrtospirifer inermis* appears first and with abundance in massive sandstones near the base of the Wiscoy formation in the vicinity of Corning, New York, and just north of Osceola across the border into Pennsylvania. Remaining fairly abundant for the rest of Wiscoy time, the species becomes rather scarce during the time of deposition of the thick sandstones that now make up much of the Canaseraga formation. In the sandstones near the base of the Caneadea formation, large, coarse-ribbed varieties appear, while the siltstones and silty shales abound in more "normal-sized" individuals. With the latter are found *C. hornellensis* and possibly exotic elements. The middle half of the Caneadea shale is once more poor in any cyrtospirifers (but rich in *Tylothyris mesacostalis*). Average-sized forms again predominate in the upper quarter of the Caneadea formation. These changes may best be seen in the Greenwood-Angelica areas of New York State. In the same vicinity, *Cyrtospirifer sulcifer* (Hall) first appears in the upper part of the Rushford sandstone, while at the same time *Cyrtospirifer inermis* decreases greatly in numbers. The two species are found together only in a limited zone at the beginning of the dominance of *C. sulcifer.*

Following upon the range of *C. sulcifer* through the Machias, Cuba, and the greater part of the Volusia formations in the area of Olean, *Cyrtospirifer inermis* continues to the top of the "Chadakoin" formation. It seems, as well, to have crossed over into the Panama conglomerate, the lowest unit of the Conewango Series, in the same vicinity, but is not found any higher. Far to the west, however, in the Corry-Meadville region this species carries through into the Amity shale as well, and possibly ranges up to the top of the Conewango Series.

Cyrtospirifer sulcifer (Hall)

Plate 5, figures 1 to 13; Plate 6, figures 5 and 6.

Spirifera disjuncta Hall, 1867, [non Sowerby], Pl. 41, figs. 10 to 16.
Spirifera disjuncta Hall, 1883, [non Sowerby], Pl. 55, fig. 16.
Spirifer disjunctus var. *sulcifer* Hall and Clarke, 1894, Pl. 30, fig. 16.

Description. Shell medium to large, subquadrate to semicircular in outline.

Pedicle valve with greatest arching toward the umbo. Lateral slopes gently convex, generally slightly depressed for about the last one-third of the distance to the extremities. Sinus shallow, rounded, well-defined, and, in many specimens, with a median groove, corresponding to a similar groove on the fold of the

opposite valve. Delthyrium about as wide as high, closed by secondary calcitic growth from the base of the dental lamellae and the floor of the shell in the beak region. Dental lamellae divergent, extending for one-third or up to one-half the length of the shell. Muscle scar ovate, broad toward the front, and longitudinally striate, not generally well-defined, however.

Brachial valve convex, with similar, although less pronounced, arching as that of the pedicle valve. Fold well-defined to the beak, rounded, and always with pronounced median groove extending its length. Tooth sockets and hingeplate rather small. Brachial muscle scar not prominent.

Exterior covered with round-topped costae, simple on the lateral slopes, but bifurcating on the sinus and fold. Costae average about 24 on each side. In the sinus, bifurcation takes place most often in the costae of the median division, for, as in many other of the cyrtospirifers studied, two primary costae arise first, and remain simple for the length of the sinus. In the central division between these, a median costa arises, and bifurcates almost immediately. Further splitting takes place in the two costae thus created and in their branches. New costae arise from the sides of the sulcus, as well. Only fine growth lines are present as micro-ornament.

Discussion. The unique median groove on the fold, and, in many specimens, in the sinus as well, distinguishes this species from all others.

In size and shape, *Cyrtospirifer sulcifer* varies considerably. In the Cuba sandstone, many large specimens are to be found (Pl. 6, fig. 6), while contrasting, small, flat, mucronate varieties may be found in shales of the Volusia formation. The close resemblance of the latter to the shape of *Cyrtospirifer hornellensis* (n. sp.) may be an example of adaptation to similar environments inducing a similar morphology.

Distribution. Most common in the Cuba formation and the lower part of the Volusia shale of the Olean area, this species is found first in the upper part of the Rushford sandstone farther east. Its upper limit is found somewhat below the base of the Hinsdale sandstone, in the Volusia formation.

The species does not seem to have had a wide westerly range; specimens collected farthest to the west were from Volusia beds just above the Cuba, in the stream north of Albion, New York. Although Caster reported and figured a specimen from the "first Venango sandstone" (probably the Corry) (1930, Pl. 4 (25), fig. 7), it is felt that in his case, as in other rare examples from beds much lower, an example of a mimicking variety of another species is being dealt with. The species proper occupies a restricted stratigraphic, and probably geographic, zone. For this reason, as well as for its unique morphologic features, it is considered to be of specific rather than varietal rank.

Cyrtospirifer vandermarkensis n. sp.

Plate 6, figures 7 to 12.

Delthyris cuspidata Hall, 1843, p. 270 (partim).

Description. Shell large, very wide, trigonal in outline.

Pedicle valve with greatest arching at the beak; lateral slopes very gently convex. Sinus of moderate breadth, rounded, and well-defined from the beak. Umbo projecting well beyond the hingeline, and slightly incurved. Cardinal area very high and extending to the extremities, with its upper margins almost straight. Delthyrium about as broad as high, with about its upper two-thirds

closed by secondary calcitic growth from the floor of the beak region of the shell and the bases of the dental lamellae. Dental lamellae very brief, restricted to the beak, and divergent. Muscle scar almost circular, longitudinally striate, limited behind by the dental lamellae, and always quite prominent. In older individuals, it is deeply embedded in secondary shell material. Teeth short and stout.

Brachial valve convex, with greatest arching at the beak. Fold narrow, rounded, and well-defined to the beak. Umbo projecting a little beyond the hingeline. Cardinal area low, vertically striate, and extending the full width of the valve. Tooth sockets short, wide, and brief; crural plates stout.

Exterior of both valves covered with numerous fine, round-topped costae, of which all but those closest to the sulcus and fold begin at the hingeline. No microornamentation, other than growth lines, has been observed.

Discussion. This species resembles *Cyrtospirifer chemungensis* (Conrad) in having very restricted dental lamellae, a subcircular muscle scar, and very numerous fine costae, many of which begin at the hingeline. It differs significantly, however, in lacking the greatly extended mucronate extremities. Furthermore, the lateral commissure in this species is not straight, but gently convex, the cardinal area is much higher, the delthyrium is largely closed, and the distinctive, subangular margins to the sinus, which is so distinctive a feature of *C. chemungensis*, are lacking in *C. vandermarkensis*. *C. altiplicus*, also a many-ribbed, wide form, has a very high fold and broad sinus, and much more extended dental lamellae. It also has very mucronate extremities not present in this form.

Distribution. This species was found only in a stratigraphically restricted zone near the top of the Machias formation, hence lies some 1000 feet higher in the section than the somewhat similar *Cyrtospirifer chemungensis*. Specimens have been collected from Vandermark Creek, near Scio, New York (also James Hall's collecting locale), and from just south of Machias, New York. In the latter place, the zone lies some 25 to 50 feet higher in the section than it does at Vandermark Creek. This is to be expected if the zone of *Cyrtospirifer vandermarkensis* is one of approximate time equivalence.

Cyrtospirifer hornellensis n. sp.

Plate 7, figures 1 to 7.

Description. Shell small, mucronate, rather thin.

Pedicle valve with greatest arching at the umbo. Transverse arching decreasing from the sinus outwards, becoming slightly concave near the extremities. Sulcus shallow, well-defined, and widening progressively forward, giving it bow-shaped boundaries. Umbo projecting beyond the hingeline slightly. Cardinal area curved, vertically striate, and narrowing rapidly toward the extremities. Delthyrium about as broad as high, closed for about the upper one-third by secondary calcification from the floor of the shell and bases of the dental lamellae. The latter structures extend forward well into the body of the shell for about one-third its length, and are initially divergent, becoming almost subparallel. Muscle scar spatulate, its posterior portion enclosed within the dental lamellae.

Brachial valve gently and evenly convex, thin. Fold shallow, well-defined, and expanding toward the front of the shell in a manner complementary to that of the sinus. Transverse arching similar to that of the pedicle valve. Umbo small, projecting very slightly beyond the hingeline. Dental sockets narrow and small.

Exterior of both valves covered with fine costae, with 20 to 25 simple costae on each lateral slope (average: 24), and bifurcating costae on the sinus and fold. Costae in the sinus bifurcate in the following manner, in those specimens studied: after the first primary costae divide the sinus into three divisions, new costae arise from the lateral margins of the outer divisions, while the actual bifurcating takes place in the central portion, principally in the median and admedian costae. At about one-half the shell length, the two primary costae may undergo division, as well. By the time the front of the shell is reached, the sulcus contains a large number of fine ribs.

A finely spinose micro-ornament covers the surface of *Cyrtospirifer hornellensis* (Pl. 7, fig. 7).

Discussion. The size and shape of the shell of this species, its fine costae, with distinctive micro-ornament, and the way in which the sinus and fold expand anteriorly, serve to distinguish this form from anything else found in the Catskill Delta. It somewhat resembles the descriptions of *C. animasensis* Girty of the far west (the latter, too, seems to be largely confined to a shale facies), but differs from it in having mucronate extremities, a curved cardinal area, distinctive fold, and spinose micro-ornament.

Cyrtospirifer preshoensis (n. sp.), like the present species, has a spinose ornamentation, but on it the spinules are much coarser and more regularly arranged. The gross shell morphology of these two species is quite dissimilar, and their lithofacies contrastingly different.

The species is named from the city of Hornell, New York, in which vicinity it is found in greatest abundance.

Distribution. *Cyrtospirifer hornellensis* is a facies fossil, being found in large numbers in the shales of the Wiscoy formation. It was first found in a shale sequence 140 feet below the top of the Wiscoy formation near Hornell, New York. This stratigraphic interval approximately correlates with a part of the zone in the Elmira-Corning region in which a great diversity of "*Spirifer disjunctus*" is found. The species ranges upward through the shales and sandstones of the Wiscoy formation, and through the Canaseraga, which is predominantly a siltstone and sandstone unit, and in which the species is quite scarce. Specimens may also be found in the lower part of the Canisteo shale formation. The highest occurrence, although much farther west in the vicinity of Machias, New York (hence not separated by as great a time as stratigraphic interval, from the eastern zones), was in the lower part of the Machias formation, again a dominantly shale unit (see fig. 3).

Cyrtospirifer nucalis n. sp.

Plate 7, figures 8 to 20.

Spirifera disjuncta Hall, 1867, [non Sowerby], Pl. 42, figs. 1, 2(?), 4(?).
Spirifer disjunctus Hall and Clarke, 1894, [non Sowerby], Pl. 30, fig. 16.

Description. Shell small, obese, umbonate.

Pedicle valve with greatest arching at the beak, and markedly so. Lateral slopes convex outwards to the extremities, where slight concavity occurs. Sulcus narrow, fairly well-defined and markedly V-shaped in cross-section, rather than rounded (Pl. 7, fig. 18). Umbo projecting greatly beyond the hingeline. Cardinal area high, curved, narrowing abruptly toward the extremities. Delthyrium about as broad as high, on the average, but much narrower in some individuals, and

closed by secondary growth from the sides of the aperture and floor of the shell, as shown in Plate 7, figures 16, 17, and 19. Dental lamellae divergent, extending forward almost one-half the shell length. The beak region is generally heavily calcified by secondary growth, which thickens the bases of the dental lamellae, and unites them to similar material closing the delthyrium from its sides. Muscle scar broadly spatulate, longitudinally striate, and with some differentiation of the median adductor scar. A spear-like apical boss or callus of secondary growth between the bases of the dental lamellae is present. Teeth are not prominent.

Brachial valve convex, but much less arched than pedicle valve. Fold fairly prominent, rounded, well-defined. Umbo projecting slightly beyond the hinge-line. Dorsal cardinal area rather high. Dental sockets shallow, but with stout hingeplates. Brachial valve muscle scar poorly defined.

Exterior covered by rather low, broad, rounded costae, simple on the lateral slopes, but bifurcating on the fold and sulcus. Costae average 20 each side, but many specimens have as few as 15 of these. The outermost earlike extension does not appear to have costae, or else they are so fine as to be poorly preserved. Fine lines of growth are present as micro-ornament.

The two primary costae generally remain simple and more prominent for the length of the sinus. In many specimens, however, an early bifurcation in these ribs takes place, with the branches closest to the midline remaining weaker and finer than the main branch. The latter then remains simple for the rest of its length. In the two lateral divisions, bifurcation first takes place in the two costae which appear initially in those sections, with new ribs also arising from the sides of the sulcus. About an equal amount of bifurcation occurs in the costae of the central division of the sinus to that in the lateral divisions.

Discussion. The size and shape of the shell, obesity, greatly arched pedicle valve, V-shaped sinus, and broad ribs are distinctive of the species, and serve to distinguish it from *Cyrtospirifer inermis*, with some of whose variants it could conceivably be confused. Very probably the latter is its nearest relative. The number of lateral costae, and the muscle scar are also diagnostic for this species.

The name is derived from the supposed resemblance to a nut.

Distribution. *Cyrtospirifer nucalis* has been found only in a few thin zones in the Conneaut Stage. The lowermost, in the Volusia formation, was found at Ellington, New York, and traced westward to the Jamestown shale quarry. An upper zone seems to be much more widespread. It has been traced from near Ceres, New York, to north of Olean, where it lies some 45 feet below the chocolate-colored shale (Butts' zone 10, 1902, p. 990), and about the same distance above the Hinsdale sandstone. Just south of Humphrey, New York, these forms are found within the chocolate shales, as they also are at a locale 1.5 miles southeast of Carrollton, New York. Next farther west, they were found at the highest point of the road up Jersey Hollow, near Cattaraugus, New York, but now stratigraphically higher in the "Chadakoin" formation. Farthest west of all, these distinctive cyrtospirifers occur near the Pennsylvania border north of Sugar Grove, once more in a chocolate-colored shale sequence in the "Chadakoin," but now only about 50 feet below its top. Since very few of these fossils were found above, nor yet below for some 300 feet of section, it appears likely that but a single zone is here represented. All collecting points lie essentially on a plane (see fig. 4). Hence, it seems that a horizon of approximate time equivalence is met with.

The significance, if any, of the close association of *C. nucalis* with chocolate-colored shales is not known.

Cyrtospirifer tionesta n. sp.

Plate 8, figures 1 to 12.

[?] *Spirifer disjunctus* Hall, [non Sowerby], Caster, 1930, Pl. 3 (24), fig. 5.

Description. Shell of a size and shape well-shown in figures 3, 4, and 6, Plate 8. Pedicle valve with greatest arching at the beak, moderating toward the front of the shell. Lateral slopes convex, becoming slightly depressed for about the last one-quarter of the distance to the extremities. Sulcus shallow, broad, not well-defined but inflecting outwards onto the lateral slopes. Cardinal area fairly high (about 1:4, to width), gently curved, and vertically striate (about 40 striae per cm.). The area extends to the extremities, narrowing gradually. Delthyrium generally higher than wide and closed for the upper one-half or more by secondary growth from the floor of the shell, and the bases of the dental lamellae. The latter commonly extend well into the body of the shell, but are rather variable. Always initially straight and divergent, in some specimens they may become subparallel, and continue forward as a low, slender ridge which converges and unites at the front of the muscle scar. The latter is ovate or spatulate, generally expanded somewhat at the front, and has striae which apparently radiate from near the posterior of the scar, those toward the rear deflecting laterally near the edges of the muscle area. The adductor muscle scar is fairly well-defined as a slender groove down the center of the larger cicatrix. An "apical callosity" is always more or less prominent. Fibrous, secondary shell growth is mainly confined to the hinge area lateral to the dental lamellae. Teeth are rather small.

Brachial valve convex, and gently arched from front to rear. The fold is very well-defined from the beak, and is rather high, narrow, and bounded at the sides by pronounced grooves. The lateral slopes are gently convex, flattening near the extremities. The dorsal muscle scar is not pronounced. Dental sockets small, but with rather stout crural plates.

Exterior of both valves with very broad, flat-topped or slightly rounded costae, separated by very narrow, round-bottomed grooves. Costae are simple on the lateral slopes, but bifurcate after a general pattern in the sinus. In this, the median costa of the sinus bifurcates initially and very shortly after its emplacement between the two primary costae. Then its branches divide, and these again divide, and so on repeatedly. Bifurcation is rather uncommon in the two primary costae and in the costae of the lateral divisions. In the latter segments of the sinus, new costae arise from the borders of the sulcus. Costae on the lateral slopes number about 25 or 30 each side. Fine, distinctive, undulating lines of growth are present as micro-ornament (Pl. 8, fig. 7).

Discussion. This species is characterized by the size and shape of its shell, by the broad, flattish, costae with their fine, concentric growth lines, by its wide, poorly defined sinus, with narrow, well-defined fold, and by the radiately striate muscle scar. The wide, gently rounded sinus, broad costae with their distinctive micro-ornament, and different muscle scar especially serve to distinguish this species from *Cyrtospirifer inermis*, which is probably its closest relative.

The shape of the shell, broad sinus, and utterly different cardinal extremities

contrast with similar structures present in *Cyrtospirifer corriensis* (n. sp.) and *C. spicatus* (n. sp.). The shape of the shell, broad costae, poorly defined brachial muscle scar, and smaller hingeplates differ from corresponding structures in *Cyrtospirifer oleanensis* (n. sp.).

This species seems to bear some resemblance to *Cyrtospirifer kindlei* Stainbrook, found in the Percha formation of New Mexico and Arizona, in size, in having a wide, shallowly rounded sulcus, and in having broad, flat-topped costae with fine growth lines (Stainbrook, 1947, p. 318, Pl. 44, figs. 1, 2, 7–12). It differs from the published description of *C. kindlei*, however, in its more-extended cardinal extremities and lesser obesity; differences too great, apparently, to be merely of varietal significance.

There is a possibility that species allied to *C. tionesta* occur in other parts of the world. For instance, there is a superficial similarity of our form to some illustrated by Sowerby (1840, Pl. 55, figs. 2 and 3), and by Whidborne (1897, Pl. 18, fig. 12). Their specimens were obtained from English localities.

The specific name has been derived from the town of Tionesta, Pennsylvania, in whose vicinity numerous fine specimens may be collected.

Distribution. The range of *Cyrtospirifer tionesta* apparently begins with the Panama conglomerate, the basal formation of the Conewango Series, in the Olean area of New York. However, poorly preserved fossils, possibly of this species, have also been located in the upper Conneaut beds. Occasional specimens may be found throughout the formation which succeeds the Panama, the Cattaraugus. In this area around Olean, so far as known, it does not carry through into the Oswayo formation. This is not true farther west, however, for in the vicinity of Warren, Pennsylvania, the species ranges upward through the Oswayo shale as well, and still farther west, in the meridian of Jamestown-Tionesta, the same species may be found throughout the Riceville and Cussewago Stages, and as high as the Corry sandstone. In the region of Meadville, Pennsylvania, it is found yet higher, ranging almost to the top of the Orangeville formation—the highest stratigraphically that "*Spirifer disjunctus*" was collected.

Cyrtospirifer spicatus n. sp.

Plate 9, figures 1 to 8.

Spirifera disjuncta Hall, 1867, [non Sowerby], Pl. 42, figs. 13 and 19.
Spirifera disjuncta Hall, 1883, [non Sowerby], Pl. 55, fig. 14.
Spirifer disjunctus Hall and Clarke, 1894, [non Sowerby], Pl. 30, fig. 14.

Description. Shell medium to large, with greatly attenuate mucrons, as well-shown in figures 1–8, Plate 9.

Pedicle valve with greatest arching at the umbo, moderating towards the front of the shell. Sulcus wide, shallow, fairly well-defined. Umbo projecting beyond the hingeline, rather pointed and incurved. Cardinal area curved from about vertical to parallel with the plane of the valve, vertically and transversely striate, and extending far out along the mucronate extremities. Delthyrium as wide as, or greater than, its height, and closed for about the upper one-third by secondary calcitic growth. Dental lamellae moderately extended forward into the shell (about one-third the shell length), and diverging at about a 45-degree angle. Muscle scar ovate or spatulate, partly enclosed by dental lamellae behind, and faintly radially striate from about the center of the scar. A long, slender median adductor muscle scar can be distinguished in some specimens. A low "apical callosity" of secondary growth is commonly present at the posterior end of the

muscle scar. More fibrous growth material builds up the shell in the areas outside the muscle scar.

Brachial valve convex, much less arched than the pedicle valve. Fold evident from the beak, low, rounded, and well-defined by lateral grooves. Umbo small, projecting only slightly beyond the hingeline. Tooth sockets small. A low, slender median ridge is present in the brachial valve of some individuals.

Exterior covered with numerous, rather broad, rounded costae, simple on the lateral slopes, bifurcating on the fold and sulcus. In the sulcus, the median costa, those adjacent to it, and the two primary costae are all seen to bifurcate. However, the most frequent bifurcation takes place in the median and admedian costae. An average number of 35 costae are present on each lateral slope, of which the last ten or so appear to begin at the hingeline, the others in the region of the umbo. Fine growth lines are present as micro-ornament.

Discussion. The most obvious feature distinguishing this from all other species is the spike-like extensions to the hingeline, which unite to the sub-semicircular main body of the shell at a fairly sharp angle. The broad ribs covered with fine growth lines differentiate this species from the other cyrtospirifers described, with the possible exception of *C. tionesta*. The mucronate extremities as well as the more pointed and incurved beak, which is quite different from the blunt, rounded one of the last-named species, make the two forms readily distinguishable.

The specific name for this form has been derived from the characteristic, spike-like mucrons which it possesses.

Distribution. The most easterly occurrence of *Cyrtospirifer spicatus* so far located is in the well-exposed quarry in the Amity shale one mile north of Corry, Pennsylvania. Thence westward to the Cambridge Springs, Meadville, and Cussewago River areas it is to be found ranging upward through the shales and thin sandstone beds of the Salamanca, Saegerstown, and Oswayo formations of the Conewango Stage. In Ohio, in Chippewa and Brandywine Creeks south of Cleveland, it is to be found in shales and argillaceous limestones of the upper part of the Chagrin shale.

It seems, therefore, that this species shows a marked affinity for the shale facies.

Cyrtospirifer corriensis n. sp.

Plate 10, figures 5 to 14.

[?] *Spirifer disjunctus* Hall, [non Sowerby], Caster, 1930, Pl. 3 (24), figs. 3 and 9.

Description. Shell large, subquadrate, obese, with small angular extremities.

Pedicle valve obese, moderately to greatly arched, more so toward the beak. Lateral slopes convex. Sulcus deep, rounded, fairly well-defined, beginning at the beak. Umbo projecting beyond the hingeline, and incurved. Cardinal area high, not markedly striate, curving through an angle less than 45 degrees. Area narrowing abruptly toward extremities. Delthyrium of greater height than width, closed for about upper one-third by secondary calcification. Dental lamellae extend forward into the shell for about one-third or one-half its length, are initially divergent, but become subparallel. In some individuals, they are continued forward as a low, slender ridge, converging and uniting around the front of the muscle scar. The latter is elongate and spatulate, with a very marked, slender, longitudinally striate adductor scar extending almost throughout the

length of the main scar. Outside of this, the main area of the cicatrix is faintly radially striate from its approximate center.

Brachial valve obese and greatly arched, more so toward the beak. Fold prominent, rounded, beginning at the beak, and bounded at the margins by well-defined grooves. Umbo rounded, and projecting slightly beyond the hingeline. Tooth sockets small, with rather stout, horizontal hingeplate. Costae broad, rounded, simple on the sides of the shell, bifurcating on the fold and sinus. Bifurcation in the sulcus takes place mainly in the median area between the two initial primary costae. The latter generally remain simple throughout their length, although one specimen appeared to have a bifurcation in one of these at about one-half the shell length. One costa arises in the median area, and bifurcates almost at once, then its branches generally bifurcate (especially those toward the midline), and so on repeatedly. Bifurcation in the areas outside the two primary costae is apparently rather uncommon, hence there are a great many more ribs near the midline of the sinus than elsewhere. In the lateral divisions just mentioned, costae arise from the sides of the sinus, and, as they generally remain simple, they are broader than those near the midline. Costae on the fold also bifurcate greatly, but apparently in a more haphazard fashion. Costae average 24 on each lateral slope. Some shells have rather prominent growth lines, giving a rugose appearance to the surface.

Discussion. This species may be easily distinguished from *C. tionesta* by the square-cut shape of its shell, its greater obesity, and the coarse, round-topped costae, which lack the fine growth lines of the latter. It also shows less variation in the dental lamellae, for these are invariably long and subparallel. However, in view of their possession of somewhat similar features—broad costae, radially striate muscle scar, high, narrow delthyrium, prominent fold, and manner of bifurcation of the costae of the sinus—it is not unlikely that the two species are closely related. Their proximity in space and time would seem to support this opinion.

Cyrtospirifer warrenensis (n. sp.), like *C. corriensis* a large, broad-ribbed form, has shorter, widely divergent dental lamellae, which enclose a much broader, ovate muscle scar. *C. warrenensis* is commonly a much larger and wider form as well, and the umbo of its brachial valve is commonly broader and more projecting than in *C. corriensis.*

Corry, Pennsylvania, in whose well-exposed shale quarry this form is common, has provided a suitable name for the species.

Distribution. The most easterly, presumably earliest, occurrence of this species was noted near the base of the Amity shale just west of Warren, Pennsylvania. Its appearance becomes increasingly common in the Corry and Meadville areas farther west, where also its stratigraphic range augments to include the overlying Salamanca and Saegerstown formations. However, the highest occurrence of this species recorded was once more in the Warren vicinity, in the Knapp ("Marvin Creek") beds, together with *Cyrtospirifer warrenensis, C. lobatimusculus* (n. sp.), *"Spirifer" allegheniensis* Caster, and numerous syringothyrids.

It appears likely that this species is most abundant in sandy phases of the western locales, where, however, shales predominate.

Cyrtospirifer warrenensis n. sp.

Plate 11, figures 1 to 10.

[?] *Spirifer disjunctus* Hall, [non Sowerby], Caster, 1930, Pl. 2 (23), figs. 3 and 10; Pl. 3 (24), fig. 4.

Description. Shell large, subquadrate in outline, as shown in figures 3, 5, and 10, Plate 11.

Pedicle valve robust to quite obese, with greatest arching near the beak. Lateral slopes gently convex, becoming depressed near the extremities. Sinus broad, rounded, poorly defined, and starting at the beak. Umbo rounded to somewhat sharp, projecting beyond the hingeline, and incurved. Cardinal area of varying height, from quite low to very high and triangular (cf. figs. 7 and 10, Pl. 11). Delthyrium about as wide as high, closed for about its upper one-half by secondary growth from the floor of the shell and the bases of the dental lamellae. The latter greatly divergent, and extending only about one-third the length of the shell. In some specimens, they become even more divergent toward their front ends than they are initially. Muscle scar broadly diamond-shaped, large, with slender, elongate median scar for the adductor muscle showing rarely. A long, pointed "apical callus" is commonly present. Striae on the muscle scar radiate from near the posterior of the scar, hence for most of the area of the scar the latter appears to be longitudinally striate. A low, slender ridge bounds the front of the scar, and parallel to it inside the scar area, one or two low undulations are to be seen in many specimens (Pl. 11, fig. 7). Teeth short and stout.

Brachial valve convex, less arched than the pedicle valve. Fold rather high, wide, and well-defined from the beak. Umbo projecting broadly beyond the hingeline. Dental sockets short and wide, with poorly developed crural plates.

Exterior of both valves covered with very broad costae, bifurcating on the fold and in the sinus, but simple on the lateral slopes. Bifurcation takes place mainly in the costae near the median line of the sulcus, and is not common, even there. Coarse lines of growth appear on the outer margins of the shell, giving it a rugose aspect.

Discussion. The size, rugose surface features, and distinctive muscle scar are characteristic of this species. The widely divergent dental lamellae, and the shape of the muscle scar serve to distinguish this form from the generally smaller *C. corriensis*. The latter also is narrower, and has a more quadrate outline.

Distribution. This species had its greatest expansion in the Conewango Stage. It occurs in great numbers in the old quarries in the Salamanca formation at Warren and North Warren, Pennsylvania. Specimens in considerably less abundance have also been collected from the Amity shale in the Corry area farther west.

At Riceville, Pennsylvania, a few specimens were found in the Knapp formation (Cussewago Stage), and, near Titusville, a few more in the Corry sandstone (Berea Stage). In these formations the abundance of this species is greatly depleted, however.

There appears, therefore, to be a fairly restricted stratigraphic, and perhaps geographic, range to this species.

Cyrtospirifer oleanensis n. sp.

Plate 12, figures 1 to 14.

[?] *Spirifera disjuncta* Hall, 1883, [non Sowerby], Pl. 55, fig. 15.
[?] *Spirifer disjunctus* Hall, [non Sowerby], Caster, 1930, Pl. 2 (23), fig. 4.

Description. Shell medium-sized to large, wide, semicircular, with brief, acute-angled extremities, as well-shown in figures 3, 5, 10, 11, and 13, Plate 12. Some specimens, however, are of greater size, the maximum measuring about 70 mm. in width by 38 mm. in length.

Pedicle valve with greatest arching at the beak. Sulcus shallow, rounded, well-defined. Umbo projecting beyond the hingeline, incurved. Cardinal area curved, and narrowing rapidly toward the extremities. Dental lamellae restricted to the hinge area, divergent, continuing forward as a low, slender ridge, in some specimens, which further encloses the muscle scar (Pl. 12, figs. 4, 10, and 14). The latter is subcordate in outline, longitudinally striate at its anterior end, but the striae radiate outward toward the sides of the scar, at its posterior. A pointed "apical callus" divides the rear of the scar, and the entire muscle was embedded in secondary calcitic growth, hence the scar stands up on a little platform, in molds (Pl. 12, fig. 10). Delthyrium of about equal width and height, and closed for about its upper one-half, or more, by secondary growth from the base of the shell and beak region, thus forming a little callus. Teeth prominent and incurved.

Brachial valve evenly arched, its fold fairly low, rounded, well-defined, and extending to the extremity of the beak. Umbo projecting slightly beyond the hingeline. Tooth sockets curved, with small buttress plates. A prominent, horizontal hingeplate extends well into the shell cavity in distinctive fashion, as shown in figure 12, Plate 12. The dorsal muscle scar is always prominent, and is shaped as illustrated in figure 9, Plate 12.

Exterior covered with regular, rounded costae, simple on the lateral slopes, but bifurcating on the fold and sulcus. In the sinus, the two initial primary costae remain simple, with the median costa in the central division bifurcating most of all. In time of origin, the two primaries appear first, then two costae in the median division, then two more laterals just outside these, still in the median division, and finally a median costa, which proceeds to bifurcate almost at once. New costae arise adjacent to the two costae bounding the sinus, as well. The lateral costae average about 24 in number, on each side. Growth lines appear to be the only micro-ornament present.

Discussion. The large, distinctively shaped hingeplate is unique among the forms of the "*disjunctus*" tribe studied. "*Spirifer*" *allegheniensis* has a similarly shaped and deeply embedded muscle scar, and restricted dental lamellae, besides having a somewhat similar semicircular outline. However, in that species the ribs are much coarser and fewer in number, the entire surface more rugose, some of the lateral costae bifurcate, and the brachial muscle scar is much less prominent (see Pl. 9, figs. 10 to 13).

Cyrtospirifer inermis generally has longer dental lamellae, has a much less prominent brachial muscle scar, and does not have the large hingeplate of this species. *C. oleanensis* is also of a different, wider shape. It is not unlikely, however, that the two species are closely related, since their ventral valves are some-

what similar, and their methods of costation and bifurcation somewhat resemble each other. Since *C. oleanensis* has a higher, fairly well-defined stratigraphic range, and possesses unique morphological characters, sufficient basis for the erection of a new species is thought to exist.

The specific name has been derived from Olean Rock City, New York, in which vicinity many excellent specimens have been collected.

Distribution. *Cyrtospirifer oleanensis* occurs rarely in the Saegerstown shale of the Conewango Series, in which it has been found west of Warren, Pennsylvania. At the base of the Oswayo formation (Roystone coquinite) in the area around Olean, New York, the species is dominant among the spiriferid shells. In the same general area, it ranges through the Oswayo formation and into the Knapp conglomerate (basal Mississippian) without significant morphologic change. The species has also been found in exposures of the Oswayo shale along the highway west of Ludlow, Pennsylvania. Just west of Warren, however, *Cyrtospirifer tionesta* largely replaces it in this formation. In the basal Oswayo bed of the Olean region and elsewhere, both *C. tionesta* and *C. oleanensis* are found together, a situation that is also true for the Knapp conglomerate and the Corry sandstone from the Garland area westward at least as far as Titusville, Pennsylvania.

Cyrtospirifer leboeufensis n. sp.

Plate 13, figures 1 to 9.

Description. Shell of medium size, pentagonal in outline, as shown in figures 6 and 7, Plate 13.

Pedicle valve with greatest arching at the beak. Transverse slopes gently convex, flattening near the extremities. Sinus shallow, wide, rounded, poorly defined, grading outwards onto the lateral slopes without much angulation. Umbo broad, projecting far beyond the hingeline, incurved. Cardinal area high, curved, changing from almost vertical to almost parallel with the plane of the shell, and narrowing abruptly toward the shoulders. Delthyrium rather higher than broad, closed in upper one-half by calcitic growth. Dental lamellae extending well into the shell, subparallel, converging, and continuing forward as a low, slender ridge which joins around the front end of the muscle scar. The latter is spatulate, with a slender median groove for the adductor muscle confined between two long, thin, very low ridges. The posterior one-third, or so, of the scar area is smooth, probably due to secondary shell growth, while the remainder is radially striate from about the center of the scar. The entire scar bounded by the dental lamellae and anterior ridge extends far into the shell for from one-half to two-thirds the shell length.

Brachial valve with convex sides. Fold rather low, rounded, and well-defined from the beak. Umbo projecting slightly beyond the hingeline. Tooth sockets long, curved, with stout buttress plates. Crural plates poorly developed (Pl. 13, fig. 1).

Exterior of both valves with simple costae on the sides of the shell, bifurcating on the sinus. The costae are low and rounded, and the surface of the shell appears fairly smooth, in many of the molds found. In the sinus of one specimen, two primary costae appear first of all, followed by two interior laterals in the median division, then by two more inside those. Two costae in the lateral divisions appear next, and then the first bifurcation takes place in the two costae adjacent to

the midline. With further bifurcation of the median costae, and additional members arising in much the same way as earlier in the shell's growth, the sinus comes to bear many fine costae near the front of the shell.

Discussion. The distinctively marked, elongate muscle scar, partly enclosed by the two subparallel dental lamellae, together with the size and shape of the shell, make this species easily distinguishable from anything else found in the Upper Devonian-Lower Mississippian strata of New York and Pennsylvania. A somewhat similar scar and dental lamellae are present in *Cyrtospirifer corriensis*, but the larger size, square outline, obesity, and more rugose surface of the latter are utterly different. Also distinctive for this species are the broad, shallow, poorly defined sulcus, broad umbo, high, curved cardinal area, and the manner of bifurcation of the costae in the sinus.

The shape of the shell and the convergent dental lamellae might make one consider whether these shells possibly belong to the genus *Cyrtiopsis* Grabau (1931, p. 421–492, Pls. 45–50). However, as in the case of *Cyrtospirifer preshoensis*, the lack of an apical foramen above a convex deltidium, and of fine, radiating surface liration rules out the possibility.

The name given to this species is derived from the LeBoeuf quarry where these shells are quite common.

Distribution. *Cyrtospirifer leboeufensis* was found in the lower part of the Amity shale of the Conewango Stage one mile north of Corry, Pennsylvania, and in the LeBoeuf quarry near LeBoeuf, Pennsylvania. In the fossiliferous uppermost few feet of the Chagrin shale south of Cleveland, a few natural casts with the distinctive muscle scar of this species have also been collected.

Cyrtospirifer lobatimusculus n. sp.

Plate 13, figures 10 to 20.

Spirifera disjuncta Hall, 1867, [non Sowerby], Pl. 42, fig. 3.
Spirifera disjuncta Hall, 1883, [non Sowerby], Pl. 55, fig. 17.
[?] *Spirifer disjunctus* Hall, [non Sowerby], Caster, 1930, Pl. 3 (24), fig. 6.

Description. Shell of a rather distinctive, trapezoidal shape, as illustrated in figures 10, 15, and 19, Plate 13.

Pedicle valve with slightly greater arching at the beak. Lateral slopes convex, becoming slightly depressed near the extremities. Sinus shallow, rounded, not well-defined at the sides, but extending to the beak. Umbo projecting beyond the hingeline, incurved. Cardinal area high, curved, narrowing evenly toward the extremities. Delthyrium somewhat higher than broad, generally, and closed for about the upper one-third by secondary calcification from the floor of the beak region and the bases of the dental lamellae. The latter extend into the shell about one-third of its length, and are initially divergent, becoming slightly incurved and low, at their front. Beyond these, the muscle scar is further enclosed by a low, slender ridge, which does not simply form a rounded front to the scar, but expands forward into a distinctively fashioned lobe (Pl. 13 figs. 10, 18, and 19). Muscle scar radiately striate from very near its posterior end, hence appearing to be longitudinally striate for most of its length. An apical boss or callus is always present, and a slender scar for the adductor muscle is differentiable, in some individuals.

Brachial valve with convex lateral slopes which become slightly depressed near the extremities of the shell. Fold rather high, rounded, and well-defined for

the length of the shell. Umbo projecting beyond the hingeline. Dental sockets rather large, but with poorly developed buttress plates and crural plates (Pl. 13, fig. 12).

Exterior covered with broad, rounded costae, which bifurcate only on the fold and sinus. An average of 24 costae are present on each side of the shell. On the fold and sinus, the costae bifurcate much less frequently than in most of the other forms of *Cyrtospirifer* studied, hence the costae are not very much finer in those places than on the lateral slopes. The two initial primary costae remain simple for their entire length; the costa nearest to the midline is the one commonly seen to bifurcate. Growth lines are generally prominent.

Discussion. The form of the muscle scar in this species is unique, and is useful in separating it from all others; from its lobate shape the specific name has been derived. The distinctive outline and the size of the shell also help to distinguish this form from *Cyrtospirifer tionesta*, *C. spicatus*, *C. corriensis*, *C. warrenensis*, and *C. oleanensis*. The muscle scar and much coarser costae differentiate it from *C. inermis*, while the greater number of lateral costae, besides many other features, will serve to distinguish this from *C. nucalis*.

Distribution. First appearing at the base of the Knapp formation (and Mississippian System) in the Warren area, *Cyrtospirifer lobatimusculus* ranges upward through the Cussewago Stage, and into the Corry sandstone, where it occurs in greatest abundance, especially in the area westward from Warren. It has been found highest of all in the Orangeville shale, which overlies the Corry, on French Creek at Meadville, Pennsylvania.

PALEOECOLOGY

PART A: RELATIONSHIP OF *CYRTOSPIRIFER* TO LITHOFACIES

As has been seen, the "*disjunctus*" tribe showed a preference for the nearshore littoral and sublittoral environment of the Catskill Delta. The question next raised is: What changes in the morphology of the cyrtospirifers can be correlated with, and considered to be an adaptation to, the sedimentary environment?

Since a sedimentary unit preserves only a partial record of its depositional environment, inferences must of necessity be made from the evidence available.

In this aspect of the study, most reliance has been placed on the excellent synthesis and reasonable inferences contained in a paper by G. A. Cooper (1937. The following is a resumé of those sections of the paper pertinent to the present work.). Study of the paleoecology of any group of animals, Cooper says, requires a paleontologist to follow several lines of inquiry:

(1) Perhaps best and easiest is comparison of fossils with recent animals of similar form and structure. This is, of course, impossible with the long extinct spiriferids.

(2) The original position of the fossil in the rock often yields a clue to its life habits.

(3) The type of enclosing sediment may tell in what kind of environment the fossil lived.

(4) Resort to paleogeography offers another method. This aspect has already been sufficiently discussed.

(5) Study of adaptations of form, ornamentation, and structure of the animals is helpful in postulating their ecology.

(6) Associated fossils may help in explaining the environment of certain forms.

Part A of the present analysis will relate to Cooper's points 2, 3, 4, and 5, while Part B will be devoted to consideration of the biotas contemporaneous with the various species of *Cyrtospirifer*.

In further discussion, Cooper states that position of the fossil in the rock is fraught with difficulties, since it is hard to be sure that a fossil has been entombed in its natural position of growth. Waves and currents play many tricks in sorting and arranging fossils. The lighter, smaller brachial valves may be almost completely swept away, leaving the heavier, larger pedicle valves behind. The latter may come to rest on the bottom with the heavier end on the mud but with the lighter anterior part of the valve off the bottom.

In deducing brachiopod habitat from the type of enclosing sediments one also meets with difficulties and dangers. The conditions of deposition of certain types of sediments, such as black shales and certain limestones, may

be open to question. Or a brachiopod shell may be found at a point far from that at which it actually lived. In general, however, brachiopods in a coarse sandstone suggest a near-shore, sublittoral zone. Heavy-shelled brachiopods have been commonly regarded as near-shore forms. Many present-day brachiopods favor hollows and sheltered places along rocky shores, and some dwell in the tide zones, where they are left out of water at low tide. This sort of environment would be represented today by conglomerates.

Brachiopods are abundant in the finer sediments in most Paleozoic formations. The ecology of these is difficult to determine, however. Generally thought to represent off-shore, deep-water sediments, paleogeographic evidence often determines them to be of near-shore origin. Although black shales may have various origins, those of the Catskill Delta were off-shore deposits accumulated in deep waters.

In morphologic adaptations, brachiopods display noteworthy homeomorphy. Cooper believes many developmental trends may be interpreted as more or less directly tending to improve or maintain the animal's ability to bring food- or oxygen-containing currents of water into the shell. The shell margin must be kept away from the bottom and out of the mud. In adapting to this necessity, the umbonal parts of the valves may become thick and heavy, so that if torn away from their place of attachment the anterior margin of the shell will come to rest above the bottom.

The development of a median fold produces a trilobate shell, thus facilitating the ingress and egress of the water currents that aerate the mantle and bring in food. In spiriferids the incoming currents are said to enter by the median fold and the unclean water leaves by the lateral flanks.

Plication has the advantage of increasing the strength of the shell.

Alation and mucronation were tendencies developed in many different brachiopod groups, reaching a maximum in the spiriferids. Forms with no pedicle opening, or a poorly functional one, would be able to develop long hinges. Auriculation or mucronation would serve to keep prone shells on the surface of the mud and out of depressions, as well as to prevent currents from upsetting the shell. Symmetrical alate forms could not develop if the shells were tightly affixed to a hard and irregular substratum.

A morphologic feature of importance, not mentioned by Cooper, is the size of the muscles which close and open the shell valves. Shells whose habitat was rigorous, with strong wave and current action, must have needed large, strong muscles, to augment the hinge articulation in preventing separation of the valves. On the other hand, animals dwelling where current action was gentle or absent would require only weak muscles. We may perhaps infer muscle size from the size of the scar area present, in fossil shells.

The cyrtospirifers of the present study, in their shell morphology and adaptations, in many ways seem to support these postulates of Cooper.

Cyrtospirifers make their first appearance in the Appalachian province in the Cayuta formation which is composed largely of siltstone and silty shale, with some sandstone beds, generally cross-laminated and lenticular. In all these beds *Cyrtospirifer chemungensis* occurs in considerable abundance

(see fig. 4). Normally, its valves are found separately, but relatively unbroken and unworn, and there is a wide range in shell size, indicating various growth stages. From this it is inferred that, although the shells were moved somewhat after death, they were not transported far, and in general were living where found. Apparently the species preferred muddy and silty bottoms where the currents were gentle. To support this, it may be noted that this species has an extended hingeline and small adductor muscles—shell features not suitable for more rigorous environments.

The succeeding Wellsburg formation is coarser and consists mainly of thin-bedded, platy sandstone, in places also cross-laminated. It suggests a cleaner, sandy sea floor on which waves and bottom currents were active and strong, sifting away the finer sediments. In these deposits, cyrtospirifers are not common. A smaller variety of *C. chemungensis* is found here, although not abundantly; one in which the shell is strengthened by fewer and much coarser ribs (Pl. 3, figs. 1 and 2).

In late Cayuta-early Wellsburg time—that is, at about the time the Highpoint formation was being deposited farther to the northwest—a variety of forms believed to belong to the species *C. chemungensis* made their appearance. A few of these are illustrated in Plate 3, figures 1 to 6. Also in the stratigraphic zone represented by this time interval, but farther west from the Chemung type area, *Cyrtospirifer preshoensis* made its first abrupt appearance.

The muddy off-shore environment during which much of the Wiscoy formation was deposited, somewhat later, bore the distinctive, small *Cyrtospirifer hornellensis.* Almost confined to the shale facies, a few specimens of this species have been located in sandstone beds as well. The small size and extended hingeline of this form would appear to suit it very well for life on a quiet, muddy or silty sea floor, which was invaded only occasionally by inundations of sand.

Also in late Cayuta time, in that part of the delta approximately lying between Corning, New York, and Sabinsville, Pennsylvania, lived *Cyrtospirifer altiplicus.* It is commonly found in well-bedded sandstone and siltstone beds. Although a wide form, like *C. chemungensis,* this species must have had a somewhat stronger shell, to judge from the longer supporting dental lamellae, greater amount of secondary calcification on the inside of the shell, and the high fold which it possessed. A stronger articulation of the valves is indicated by the larger muscle scar of this form than of those in the earlier species. From these shell features we may infer that *C. altiplicus* was well-adapted to its sandy and silty environment on that part of the delta. Thus two cyrtospirifers, *C. hornellensis* and *C. altiplicus,* contrasting with one another greatly in size, folding, mucronation, shell thickness, and micro-ornamentation dwelt contemporaneously in contrasting "adaptive zones" (Simpson, 1953) which differed greatly in lithofacies, in proximity to shoreline, in depth of water, and probably in salinity of the water, amount of sunlight, and bottom currents.

Two other cyrtospirifers made a brief appearance at about this time. Both

are found in the restricted interval of bluish shale and siltstone located just below the base of the Wiscoy formation which has been mentioned earlier. The first of these is *Cyrtospirifer whitneyi*, generally considered to be a fossil confined to the American West. Since the "bluish shale" in which it is found is equivalent to, or not far stratigraphically from, the Highpoint formation in which the only good correlation of western with eastern Upper Devonian strata can be made, the likelihood of such a migration of faunas at that time seems to be confirmed.

In the same "bluish shale" zone, *Cyrtospirifer angusticardinalis* (n. sp.) has also been found (Pl. 2, figs. 6 to 13). In appearance, this fossil is unlike almost anything else in its part of the Upper Devonian of New York and Pennsylvania. Whole specimens in various stages of growth have been collected from the shale, from which it may be inferred that this creature lived in a muddy environment, perhaps in deeper, quieter waters. Yet this species is quite unlike *C. hornellensis*, another shell presumed to have lived at the same time in quiet waters and on muddy bottoms. Its hingeline is not extended, but narrow; it is obese, instead of thin, and it lacks the finely spinose micro-ornament of the latter. Such examples emphasize the difficulties inherent in paleoecology.

In view of its abrupt appearance with no transitional forms connecting it to other species, it may be postulated that *C. angusticardinalis*, like *C. whitneyi*, and like the earlier *C. preshoensis*, is an exotic migrant, not endemic to the New York "Chemung" province.

Also in Wiscoy time, another cyrtospirifer, *C. inermis*, arrived on the scene.

Thus we can see that in Highpoint-Wiscoy time a considerable variety of forms and species of *Cyrtospirifer* appeared on the Catskill Delta. It is not generally possible to find shell forms transitional from these to earlier species of cyrtospirifers. Significant, too, is the fact that of all the cyrtospirifers that flourished on the delta, the only three species with distinctive, finely spinose micro-ornamentation—*C. hornellensis, C. preshoensis*, and *C. whitneyi*—are all found in this relatively thin stratigraphic interval. These facts, together with the already-affirmed correlation with western Upper Devonian formations during Highpoint time, make it possible to infer that some extensive barrier to migration had been removed during this interval of geologic time, permitting alien species of *Cyrtospirifer* to migrate from other faunal provinces. These new varieties and species radiated into previously unoccupied ecologic niches and into two major lithofacies.

The upper zones of the Canadaway Stage, and all of the Conneaut Stage are dominated by *Cyrtospirifer inermis*, except for a fairly brief, perhaps localized, prevalence of *C. sulcifer* and *C. vandermarkensis*. Without doubt, *C. inermis* was the most adaptive and longest-ranging of all the cyrtospirifers that lived on the Catskill Delta. After a brief "flood" in Wiscoy time, however, this species apparently did not find the sandy type of environment that prevailed during much of Canaseraga time a congenial one. In any case, *C. inermis* is found sparsely throughout the main mass of the Canaseraga sand-

stone. However, forms in considerable variety and numbers inhabited the sandy littoral zones of late Canaseraga-early Canadea time. Conspicuous among these are some very large, rather coarse-ribbed forms (Pl. 4, fig. 14, and Pl. 10, fig. 4). These we may suppose possessed a shell stout enough to withstand the buffeting of their postulated near-shore, sandy environment in which strong wave- and current-action prevailed. These large inhabitants of a sandy facies also have greatly thickened ventral umbones, a feature believed by Cooper to be an adaptation to a rigorous environment.

Individual minor variations in size, in shape of shell, in alation, in height of the fold, and in length of the dental lamellae also may be seen in this species in its occurrences in the Canadaway and Conneaut Groups. Perhaps these variations reflect many attempts of groups of individuals within the species to fit themselves into various minor ecologic niches.

In some specimens of *C. inermis* the degree of divergence of the dental lamellae seems to be a function of the width of the shell, while the latter in turn may reflect the type of bottom environment in which the cyrtospirifer dwelt.

The size of the shell in some cases may depend upon the numbers of individuals of the species which are trying to live in a narrowly circumscribed habitat. In this connection, the small, rounded form *Cyrtospirifer nucalis* may have been adapted for life in a confined space, crowded with individuals of the same species.

The variable *C. inermis* further displayed its adaptive ability in that it was the only species of *Cyrtospirifer* able to persist through into the Conewango Stage. A considerable change in sedimentation, which may possibly reflect tectonic changes as well, took place at the beginning of this stage, as evidenced by the deposition of the thick Panama conglomerate. *Cyrtospirifer inermis* may be looked upon as the spiriferid which in its morphology had best achieved harmony with the "Chemung" type of sedimentation.

At this point another change in the lithofacies of the Catskill Delta should be noted. Members of the "*disjunctus*" tribe in the Chemung Stage are commonly found in lenticular beds, in cross-bedded sandstones, and intimately associated with redbeds and flow rolls. All this betokens a near-shore environment. But the breadth of this environment, too, was now greatly restricted to a relatively narrow near-shore belt. Not far from shore the shaly facies began, in which the Chemung types of cyrtospirifers are almost totally absent (with the exception of *C. hornellensis*, as noted earlier). Gradually, however, the width of the littoral zone in which the "*disjunctus*" group could exist increased, until from about Rushford time on, these forms occupied a greatly broadened belt of littoral and sublittoral zone (see fig. 4). In this higher part of the section, flow rolls become less common, and shell-filled lenticular beds and cross-laminated sandstones are much scarcer. Instead, continuous fossil beds up to a foot or more in thickness are found here. In brief, the depositional environment had gradually changed to a broader, more shelf-like setting: probably the natural consequence of shallowing in the basin of deposition through continuous sedimentation over a

long period of time. The cyrtospirifers now found their preferred facies across a greatly widened belt along the delta.

These changes continued in the same direction for the duration of the out-building of the Catskill Delta in Upper Devonian-Lower Mississippian time, and a complementary broadening of the zone of "*Spirifer disjunctus*" keeps pace with it.

Undoubtedly one of the most important breaks in the development of the cyrtospirifer tribe took place near the beginning of the Conewango Stage. As we have seen, *C. inermis* alone persisted into the basal formation of the Conewango Stage, the Panama conglomerate, and with it there, *C. tionesta* appears. But the predominantly muddy and silty environment that followed upon the deposition of that unit, represented in its marine facies by the Amity shale, saw a notable increase in the number of species of *Cyrtospirifer*. *C. inermis* and *C. tionesta* are now joined by *C. spicatus*, *C. corriensis*, *C. leboeufensis*, and *C. warrenensis*.

It is difficult to say to what degree the appearance of these new species was due to changes in the sedimentary environment. The Amity shale is not unlike much of the (earlier) "Chadakoin" in character; we may presume it was deposited under somewhat comparable conditions. The main evidence that the environment may have altered lies in the deposition of the intervening, rather widespread, quartz-pebble Panama conglomerate. However, there is some evidence in the lithology that the various species of *Cyrtospirifer* occupied separate ecologic niches. In the Amity shale—especially as exposed at Corry, Pennsylvania, where all the Conewango cyrtospirifers may be found—each particular species is largely confined to a distinct siltstone, sandstone, or "mudstone" bed or lentil, in which the other species are quite lacking.

The long-ranging *Cyrtospirifer inermis* continued into the predominantly shale facies of the Conewango Stage, but without the phenomenal abundance it showed in the Conneaut Stage; it became in fact, relatively uncommon among the expanding abundance of its fellow cyrtospirifers. Perhaps the deposition of fine silt and muds that prevailed during this stage, now represented by the Amity, Saegerstown, and Oswayo shales, was too much even for its adaptive abilities, especially when faced with the increasing competition in almost every available ecologic niche of its more highly specialized progeny, *C. spicatus*, *C. warrenensis*, and *C. tionesta*. And this is not to mention other abundant, but probably not closely related forms, such as *Cyrtospirifer leboeufensis*, the mud-loving *Syringospira alta*, and the very numerous pelecypods. Thus *C. inermis*, too, went down to extinction.

Cyrtospirifer tionesta, in its wide range and long persistence in time, lasting through a great number and variety of formational units, showed some of the adaptable characteristics of *C. inermis*. However, in passing upward through the stratigraphic section, it is noticed that whenever a thick, fossiliferous sandstone member is met with, *C. tionesta* is less abundant than other forms of *Cyrtospirifer*. In the Salamanca formation, for instance, *C. warrenensis* predominates; in the Knapp conglomerate and the Corry sandstone, *C.*

oleanensis and *C. lobatimusculus*, along with several species of *Syringothyris*, prevail. Perhaps we may infer, therefore, that *C. tionesta* preferred the quieter waters and muddier sea floors on which the shale units were deposited.

Cyrtospirifer spicatus was apparently restricted in its range to the western shale facies, and has not been identified east of Corry, Pennsylvania. Also significant in judging its facies preferences is its presence in the shales and argillaceous limestones of Ohio. We may assume, therefore, that this species was dominantly an inhabitant of the shale facies. Certainly its elongate extremities would be useful in supporting the body of the shell above the muddy or silty sea floor on which the animals lived.

Finally, *C. leboeufensis*, an associate of *C. spicatus*, is a fairly narrow-hinged species, yet one which also could adapt itself to muddy or silty sea bottoms.

Foremost among the conclusions that may be drawn from the lithofacies studies of the Appalachian cyrtospirifers should be the extreme care that must mark the drawing of those conclusions. Most clearly defined is the fact that the "*disjunctus*" tribe preferred a near-shore habitat, in general shunning deeper waters and the black-shale lithofacies. In deltaic formations, such an environment would probably also connote abundant sunlight, and perhaps tolerance to a wide range of salinities.

The original position of the cyrtospirifers in the rock is not generally the attitude the shells had during life. Commonly, lenses consisting mainly of separated and winnowed ventral valves dominated in the earlier stages of the delta formation, with fossiliferous, well-bedded units coming in later stages. By and large, the presence of both valves, unworn, of all sizes and growth stages, in a bed containing a varied fauna, also of different sizes, indicates that, though the two valves were separated, they were found very close to or at their sites of growth.

The type of enclosing sediment in which the species of *Cyrtospirifer* were found might be summarized and tabulated as follows:

Predominantly sandstone	Predominantly shale	In both sandstone and shale
C. altiplicus	*C. chemungensis*	*C. inermis*
C. preshoensis	*C. whitneyi*	*C. sulcifer*
C. corriensis	*C. hornellensis*	? *C. allegheniensis*
C. warrenensis	*C. angusticardinalis*	
C. oleanensis	? *C. nucalis*	
C. lobatimusculus	? *C. vandermarkensis*	
	C. tionesta	
	C. spicatus	
	C. leboeufensis	

Unrecorded features of the habitat make correlation of shell morphology with environments of the past hazardous. Many distinctive features of cer-

tain species of *Cyrtospirifer* have not so far been successfully correlated with the sedimentary environment. The grove on the fold in *C. sulcifer* and the finely spinse micro-ornament in *C. hornellensis, C. preshoensis,* and *C. whitneyi* exemplify this lack; such features may be non-adaptive.

Thickness of shell and coarseness of costation distingiushes some forms living in sandy, wave-swept places. With some exceptions, such as *C. altiplicus,* these characteristics are never diagnostic of a species; they distinguish variants only.

Size of adductor muscle, as presumed from the scar size in fossil shells, has proved valuable as an ecologic indicator in *Cyrtospirifer chemungensis.* Evidence from the enclosing sediments has supported the conclusion that this individual lived on muddy or silty bottoms, and where extreme wave- and current-action was absent.

In mucronation and alation, the evidence is conflicting. Not all the species of *Cyrtospirifer* that dwelt in deeper waters on muddy bottoms possessed elongate hingelines or mucrons. Yet the examples offered by *C. chemungensis, C. hornellensis,* and *C. spicatus* indicate that, in some shells at least, the feature was adaptive to that type of environment.

It has already been observed that early in the formation of the delta, in the Chemung and Canadaway Stages, a depositional environment with a narrow sublittoral zone was present, giving way thereafter to a broader, more shelf-like setting for the rest of the out-building of the delta. We might profitably ask ourselves in just which of these depositional contexts—that with the narrow sublittoral zone or that with the wide—we are most likely to find increased speciation in a particular shell. It seems likelier that the more stable, less variable, "platform" type of environment, which would permit the widest possible commingling of different specific groups, and which would have relatively fewer ecologic niches, would tend to create fewer species than a widely fluctuating, narrow belt of more variable sedimentary character and with many more ecologic niches. This postulate is slightly supported by the present study. Early in their evolution in the Upper Devonian, there were a considerable number of species of *Cyrtospirifer,* while later on, in Conneaut time, as the more shelf-like depositional setting prevailed, one form, *C. inermis,* mainly predominated. *Cyrtospirifer nucalis,* also of the Conneaut Stage, while a specifically distinct form, hardly counts among the highly abundant and highly adaptable variants of *C. inermis.*

The adaptive alterations in *Cyrtospirifer* described above are evidence that a changing lithofacies could induce changes in morphology. But these changes were not always of specific rank nor immediate in appearance. As the Catskill Delta built outward, the type of sediment deposited formed natural lithogenetic units or formations. A considerable interval of time was needed to deposit a particular formation. The range of a particular cyrtospirifer, on the other hand, generally began or ended during a relatively brief span of time, and these beginnings or endings essentially follow the "planes of contemporaneity." Hence, the lithogenetic units—formations and

groups of formations—may be cut across by the ranges of the biologic units. (See Caster, 1930, for a discussion of the facies problems involved.)

Examples of this apparent transgression are manifold among the members of the *Cyrtospirifer* tribe (see fig. 1). *C. sulcifer,* for instance, making its earliest appearance in the Rushford sandstone in the east, seems to cut across the Machias and Cuba formations, in the lower boundary of its range, and thence up into the Volusia shale, going westward. The extensive mid-Conneaut zone of *C. nucalis* has already been observed under the distribution of that fossil, as has that of *C. vandermarkensis. C. inermis* likewise appears, in its upper range, to transgress the rock units, notably the Panama conglomerate. *C. tionesta* and *C. oleanensis,* too, are found apparently cutting across formational boundaries with no important morphologic or taxonomic changes.

The lithofacies, therefore, has at times had a profound effect upon the development of the cyrtospirifer tribe, but the character of the organism itself, especially its adaptability to changing sedimentary environments, also determines the direction and degree of change that shall be followed.

PART B: RELATIONSHIP OF *CYRTOSPIRIFER* TO BIOFACIES

The living community in which the cyrtospirifers dwelt must have played a rôle almost as important as that of the lithofacies in the evolution of the genus.

At the outset, however, we are faced with the problem of determining just what were the ecologic associates of a particular cyrtospirifer. The ecology of animal communities of the present day are often extremely complex. How much more difficult it is to determine the interrelationships of faunas that lived over 250 million years ago, and whose internal morphologies and external environments are often so largely conjectural! Still, some reasonable inferences can be drawn from the available evidence.

In the first place, although an extremely rich and varied fauna flourished on the Catskill Delta—some 1178 species have been recognized, according to Chadwick (1935)—only a fraction of these were inhabitants of the "*Spirifer disjunctus*" facies. The fauna of the black shales, at times fairly abundant, as well as that of the continental facies, can be largely ruled out as active associates or competitors with *Cyrtospirifer.* Even among its neighbors in the littoral and sublittoral zones there must have been faunal members occupying quite different ecologic niches, and having only a small influence upon the development of the cyrtospirifers.

In order to find out what its immediate associates were, the principal faunas found in the same fossil lot from the same bed with *Cyrtospirifer* have been identified. These are listed below under discussion of the different stages, and the number of collecting points at which each possibly associated fossil was found in conjunction with a *Cyrtospirifer* has been noted. The total number of points at which each species of *Cyrtospirifer* was found is entered at the top of the column for easy comparison of ratios. (A "collecting point" is defined as a particular bed at a given locality. A "collecting site"

refers to a geographic station. The latter have been located on the geologic map, figure 1.)

There are some obvious shortcomings in the method. For instance, an animal of limited abundance may have competed closely with a *Cyrtospirifer* in the same ecologic niche, and yet, simply because it was not common, it may appear only seldom in the same fossil sample. This is especially true for carnivorous forms, which always have a low ratio to their prey, and probably a contrastingly high influence upon their abundance. Likewise, an abundant faunal element, such as the crinoids, may have lived in a quite different ecologic niche, as many of them probably did, and yet, by drifting into the same death assemblage, may appear in a high number of occurrences with a particular species of *Cyrtospirifer*. A further possible source of error is in the almost unavoidable preferential collecting of samples rich in "*Spirifer disjunctus*." At each collecting point, however, a conscious effort was made to collect all the available fossils.

The species associated with a particular *Cyrtospirifer* may be viewed in two ways: first, as competitors for food, oxygen, and living space; second, as an assemblage of animals preferring a particular kind of environment which was limited by certain factors, such as temperature, pH content, amount of free oxygen, amount of light, freedom from bottom currents or the converse, microscopic food, and so on. Likewise, the absence of *Cyrtospirifer* in other assemblages may mean lack of ability to compete, or simply that some preferred environmental factors were missing.

It has been considered better to give the actual figures, rather than percentages, since the latter give a quite false impression of the data in cases where few collecting points were involved.

A greater emphasis has been placed on actual examination of the fossiliferous rock samples than upon the lists of possible associates, in analyzing the data, since a more complete record of the biofacies is there preserved.

Facies other than that containing abundant cyrtospirifers have been largely unsampled, and hence their fossils are not included in the data. Also omitted, for brevity's sake, are species that are rare. A quite complete listing of these faunas for the different stages may be found in Chadwick's excellent analysis of the subject (1935).

The material collected by the writer has formed the main basis for this phase of the study.

Chemung Stage

Of 133 collecting points in the Chemung Stage, only 61 (46 per cent) yielded cyrtospirifers. Among these, *Cyrtospirifer chemungensis* (C) appears in 36, *C. altiplicus* (A) in 13, *C. inermis* (I) in 7, *C. preshoensis* (P) in 5, *C. hornellensis* (H) in 4, *C. whitneyi* (W) in 2, and *C. angusticardinalis* (An) in 2.

Faunal associations of each species are shown in the following table in which the numerals indicate the number of collecting points at which the listed fossils occur. The first column, X, includes all collecting points with-

out *Cyrtospirifer* and each of the remaining columns represents one of the species of *Cyrtospirifer* noted above. For example, *Tylothyris mesacostalis* was found in 30 collections that lack cyrtospirifers, in 25 collections with *C. chemungensis,* in 3 with *C. altiplicus,* in 1 with *C. whitneyi,* etc.

	X	C	A	H	I	W	P	An
Tylothyris mesacostalis	30	25	3			1	2	1
Platyrachella mesastrialis	3	8			1			
Ambocoelia gregaria	25	7	2			1	2	1
Atrypa spinosa	13	26	7	1	1			
A. reticularis	3	3					1	
A. hystrix	6	4	7	1			1	
Camarotoechia contracta	11			3	5		1	1
Productella lachrymosa	25	18	8	2	6	1	2	
P. arctirostrata	2	5						
Chonetes scitulus	11	3	1					
C. setigerus	6	2				1		
Schuchertella chemungensis	12	10	5		1			
Schellwienella chemungensis	9							
Tropidoleptus carinatus	5							
Nervostrophia nervosa	5	1	1					
Leptostrophia perplana	5	3			2			
Douvillina mucronata	17	9	8	1	1		1	
Schizophoria "striatula"	21	4	2	2	4	1	3	
Dalmanella danbyi	2	2	1					
D. tioga	3			1	1			
Pterinea sp.	6	13	1					
Leptodesma sp.	18	8	1		2		1	
Aviculopecten sp.	1	2						
"Lingula" sp.	1							
Gastropoda	6	1						
"Cyathophyllum" sp.	2	2	6					
Plant fragments	3	2	2					
Bryozoa	4	2	5		2			
Crinoid columnals	24	1	6	1	3	1	2	
Tentaculites sp.	3	1	1				1	
"Orthoceras" sp.	1	1						
Cyrtospirifer chemungensis								
C. altiplicus								
C. hornellensis					1			
C. inermis				1				
C. whitneyi								
C. preshoensis								
C. angusticardinalis								

A significant fact brought out by the above analysis is the almost complete dissociation of the different species of *Cyrtospirifer* one from another. This is partly due to their nonoverlapping ranges (as with *C. chemungensis* and *C. altiplicus*) and partly to their having inhabited different facies (as with *C. hornellensis,* for instance).

By eliminating those species of the faunas that seem most certainly *not* to have been ecologic associates of *Cyrtospirifer*, a residue of those that probably were should be left. Possibly among the first so eliminated should be the dalmanellids, *Ambocoelia gregaria*, and *Tentaculites* sp., which, from their dominance in "mudstones" and shales, seem to have found niches distinct from most of the cyrtospirifers. With them, and possibly having a similar facies preference, may be excluded *Tropidoleptus carinatus*, *Schizophoria "striatula,"* the chonetids, *Nervostrophia nervosa*, and *Leptostrophia perplana*. The species of *Douvillina*, while occurring with cyrtospirifers as presumed associates, are also found in great abundance in sandstone beds wherein almost the sole associated fossil is a *Cyrtospirifer*. With the possible exception of the species of *Pterinea*, the pelecypods seem not to be found commonly with cyrtospirifers. Whether or not the clams had a preference for brackish waters, however, as has been claimed, is not brought out by the data. Fossiliferous sandstone beds including practically nothing but gastropods are found in the Wellsburg formation, but lesser numbers of snails also occur with mixed fossil assemblages, including *Cyrtospirifer chemungensis*.

From their observed occurrence with each other in fossil communities in which faunal elements of varied shapes and stages of growth are present, the probable associates of *Cyrtospirifer chemungensis* and *C. altiplicus* were *Tylothyris mesacostalis*, *Platyrachella mesastrialis*, the several species of *Atrypa*, *Camarotoechia contracta*, most of the productids, the species of *Douvillina*, *Pterinea*, gastropods, bryozoa, possibly crinoids, and "*Cyathophyllum*" sp.

The last-named of these, the cup corals, represent a unique and interesting element of the Chemung faunas. Some good zones of approximate contemporaneity have been established by correlating one or two coral beds over a considerable area. These zones have been useful in determining the stratigraphic horizon at which certain cyrtospirifers were collected in Pennsylvania where the Chemung beds have undergone considerable folding. The redbed facies is there very close to the fossil beds. In those locales at least, the cup corals dwelt very near the shoreline, probably in shallow water, where a warm, marine environment with plenty of light is inferred for them, and for *C. chemungensis* and *C. altiplicus* with which they were associated.

The previous inference based on lithologic evidence that *Cyrtospirifer hornellensis* is a shale facies fossil seems to be supported somewhat by its associates, although the few collecting points in which that cyrtospirifer was found do not permit complete certainty on this point. Apparently associated with *C. hornellensis* in the Chemung Stage were *Dalmanella tioga* and *Schizophoria "striatula,"* while in the succeeding Canadaway Stage specimens of this form were found with *Ambocoelia gregaria*, *Productella hirsuta*, and dalmanellids of species other than *D. tioga*—all forms which, from observation, seemed to favor the shale facies.

Some species that have been found abundantly in the collections, and in some cases possibly competed with *Cyrtospirifer*, or preferred the same

adaptive zones, but that did not cross over into the succeeding Canadaway Stage from the Chemung were *Nervostrophia nervosa, Leptostrophia perplana, Douvillina arcuata, D. mucronata, Dalmanella danbyi* and *Tropidoleptus carinatus.*

Canadaway Stage

Of 75 collecting points in the Canadaway Stage, 56 (75 per cent) included cyrtospirifers. Among these, *C. inermis* (I) appears in 38, *C. sulcifer* (S) in 10, *C. hornellensis* (H) in 3, and *C. vandermarkensis* (V) in 2.

Faunal associations are shown in the following table which is arranged like that for the Chemung Stage.

	X	I	S	V	P	H
Tylothyris mesacostalis	13	18	1	1	3	2
Leiorhynchus laura	3	2				1
L. mesacostale	2	1	1			
Camarotoechia contracta	7	20	5	1	3	3
Ambocoelia gregaria	5	6		1	3	2
Athyris angelica	8	10	4	2		1
Atrypa hystrix		1				1
A. spinosa					1	
Productella lachrymosa	9	21	3	2	1	2
P. speciosa	1	3	2			
P. hirsuta	1	4				2
P. arctirostrata	1	6	1			
P. lachrymosa var. *lima*		3	1			1
Chonetes scitulus	2	5	3	1		
C. setigerus	2	2	3			
Douvillina sp.		1		1		
Schellwienella chemungensis		10				1
Schizophoria "striatula"	8	9		1	2	4
Dalmanella sp.	3	3	4		1	1
Leptodesma sp.	1	7	1		1	
Pterinea sp.		6	1			1
Mytilarca sp.	2	8	2			
Other pelecypods	3	3	2		1	1
"*Lingula*" sp.	1	1				
Bryozoa	8	26	8		3	2
Crinoid columnals	7	23	5	1	5	5
Plant fragments		1				1
Gastropoda				1	1	1
Cyrtospirifer hornellensis		1			2	
C. inermis			2		1	
C. preshoensis		1				2
C. sulcifer		2				
C. vandermarkensis						

Discussion. A significant fact becoming apparent here is the high percentage of occurrences of *Cyrtospirifer* (75 per cent) in the samples collected, a phenomenon yet more noticeable in the next higher (Conneaut)

Stage. This reflects the greater abundance of the genus during this time, and possibly also the broadening, shelf-like environmental setting, which permitted a greater commingling of faunas than did the narrower Chemung littoral zone. The chances of finding a cyrtospirifer with almost any group of Canadaway fossils in a bed are thereby increased.

Again in the Canadaway Stage, as in the Chemung, the species of *Cyrtospirifer* were not commonly associated with one another. Some common brachiopod species that newly appear in the Canadaway Stage are *Dalmanella leonensis*, *Rhipidomella pennsylvanica*, *Athyris angelica*, and *A. polita*. A noteworthy number of new pelecypod species make their appearance as well, totalling 70 in all (Chadwick, 1935, p. 324–325). Disappearing in this stage were *Platyrachella mesastrialis* and *Atrypa reticularis*, both possible competitors with cyrtospirifers, judging from the similarity of their structures. *Atrypa speciosa* and *A. hystrix* are so scarce in this stage and above that they, too, must have been an insignificant element in the cyrtospirifer biofacies. All these forms had similar food-gathering mechanisms, and probably also competed with *Cyrtospirifer* in the same ecologic niches. Their decline may help to explain the expansion of the latter genus at this time.

Tylothyris mesacostalis has been generally found associated with cyrtospirifers, but also in collections where none of the latter are found. Possibly it was a wider-ranging, more adaptable form during its time of occurrence in the Canadaway Stage. The same might be true of *Athyris angelica*, and of some species of *Productella*.

Crinoid columnals and bryozoans seem to be almost ubiquitous in fossil beds of the Canadaway Stage, especially in the Machias formation, and for that reason are common associates of cyrtospirifers. Whether they were ever important associates in the same ecologic niche seems rather doubtful, however.

A rather common association of *Productella hirsuta* and *P. lachrymosa* var. *lima* with *Cyrtospirifer hornellensis*, a shale facies fossil, makes one wonder whether those species, too, may not have preferred a muddy environment.

Although too few collecting points for the species have been established, *Cyrtospirifer vandermarkensis* was found at several places with *Ambocoelia gregaria*, *Chonetes scitulus*, *Schellwienella chemungensis*, and *Schizophoria "striatula."* Possibly it may be inferred that that cyrtospirifer also preferred relatively quiet waters and muddy or silty bottoms—an inference somewhat supported by its morphology. It is a wide shell with rather weak muscular articulation (as indicated by the small muscle scar).

The commonest cyrtospirifers in the Canadaway, *C. inermis* and *C. sulcifer*, seem to be associated with *Tylothyris mesacostalis*, *Camarotoechia contracta*, *Athyris angelica*, *Productella lachrymosa*, *P. speciosa*, and possibly *P. arctirostrata*, together with some clams, bryozoans, and crinoid columnals. *C. hornellensis* seems to display a more common association with presumed shale facies forms—*Ambocoelia gregaria*, *Schizophoria "striatula,"* dalmanellids, and possibly *P. hirsuta* and chonetids. The number

of collecting points at which this cyrtospirifer was found, however, is too few for the desired degree of certainty to be established.

Conneaut Stage

Of 110 collecting points in the Conneaut Stage, 92 (84 per cent) yielded cyrtospirifers. Of these, *C. inermis* (I) occours in 65, *C. sulcifer* (C) in 21, and *C. nucalis* in 14.

Faunal associations are indicated in the following table.

	X	I	S	N
Ambocoelia gregaria	6	3	3	5
Athyris angelica	6	9	10	3
Leiorhynchus mesacostale	4	3	2	1
Camarotocchia sappho	1	2	5	
C. contracta	14	52	9	7
Productella arctirostrata	1	1	2	
P. speciosa	3	6	4	3
P. lachrymosa var. *lima*		1	2	
P. lachrymosa	5	24	9	3
P. hirsuta		5	4	3
Chonetes scitulus	3	5	13	2
C. setigerus		2	4	
Schellwienella chemungensis	1	4	4	
Schuchertella chemungensis		5	9	1
Schizophoria "striatula"	2	2		
Rhipidomella pennsylvanica (?)		3	4	
Dalmanella leonensis	2		5	2
Leptodesma sp.	5	2		2
Aviculopecten sp.	1			
Mytilarca sp.	1	8	2	2
Other pelecypods	5	9		2
Bryozoa	4	24	12	5
Crinoid columnals	9	40	14	3
Plant fragments	2	5		
"Fish bone"	3	10		1
Gastropoda	2		1	
"Orthoceras"	1			
Cyrtospirifer inermis				5
C. sulcifer				
C. nucalis		5		

Discussion. In the Conneaut Stage, there is a further increase in the number of collecting points that provided cyrtospirifers, to a total of 84 per cent. Cyrtospirifers were more abundant in this stage, and the prevalent form, *C. inermis,* was probably well able to adapt itself to the possibly smaller range of sedimentary and biologic facies of the widened, stable platform environment that now existed. The chances of its being found with almost any fossil assemblage that may be collected has again increased.

The common fossil species of this stage are much the same as those for the Canadaway.

Cyrtospirifer sulcifer, it may be noted, has associated with it a somewhat different assemblage than does its close relative *C. inermis*. With it are found greater numbers of chonetids, *Productella lachrymosa* var. *lima*, *Camarotoechia sappho*, *Schuchertella chemungensis*, *Schellwienella chemungensis*, *Rhipidomella pennsylvanica* and *Dalmanella leonensis*. From observation the two last-named of these are believed to be mainly fossils of the shale facies. (The high number of occurrences of bryozoans and possibly of crinoids is just a reflection of their great abundance in the lower part of the stage, where *C. sulcifer* also has its principal range.) Hence, there seems to be an indication here that *Cyrtospirifer sulcifer* occupied a somewhat different biological environment from that of *C. inermis*.

We may assume, perhaps, that the distinctive median groove on the fold of the former species was some adaptation to that environment. The significance of this feature in the creature's use of its habitat is not easy to to see. The groove must have been the result of folding in the front central part of the mantle, where an extra fold occurred in the brachial valve (and generally in the ventral valve as well). Some influence upon the incoming and outgoing currents of water that provided the animal with food and oxygen may have been effected by this part of the shell. If the adaptation were due to its biofacies, it is curious that the species *C. sulcifer* did not continue into the upper part of the Conneaut Stage, as its faunal associates did. In the light of present knowledge, we must consider this unique shell feature to be a possible adaptation to an unknown environmental element, or else to be a non-adaptive feature.

The great stability in biofacies during Conneaut, and much of the preceding, Canadaway time, may reflect the relative isolation of the Appalachian province during these stages. Not only do no exotic species of *Cyrtospirifer* make their appearance, but very few new species of any kind arrived during this span of time. Undoubtedly some definite but unknown barriers to migration of faunas from other parts of the world were in existence.

Conewango Stage

Of 95 collecting points in the Conewango Stage 71 (75 per cent) yielded cyrtospirifers. Among these, *C. tionesta* (T) occurs in 34, *C. warrenensis* (Wa) in 15, *C. corriensis* (Co) in 11, *C. spicatus* (Sp) in 11, *C. oleanensis* (O) in 7, *C. leboeufensis* (L) in 6, and *C. inermis* (I) in 5. "*Spirifer*" *allegheniensis* (Al) occurs in 6.

Faunal associations are shown in the following table.

Discussion. Only 75 per cent of the collected samples from Conewango strata contained cyrtospirifers, compared with 84 per cent from the Conneaut Stage. This, too, is in spite of the greater number of species in the higher stage.

The most abundant new brachiopod occurring in the collections from the Conewango Stage is *Camarotoechia allegania*, a form characteristic of the

	X	T	I	Wa	Co	L	Sp	O	Al
Ambocoelia gregaria		3	2		1	4	3		
Athyris angelica		1	1			2	2		
A. polita			1			2	2		
Leiorhynchus laura						1	1		
L. mesacostale	1	1	1			1	1		
Camarotoechia allegania	6	3		1	1		1	4	
C. orbicularis	3	3	2	4	2	2	4		1
C. contracta	7	13	3	6	2	4	4	2	
Strophalosia hystricula		1	1	1	1		2		
Productella bialveata	1	3		1			1		
P. lachrymosa	1	4		1		2	5		1
P. hirsuta	3	5	2	3	1	4	7		
Chonetes scitulus	3	6	2	4	2	2	4		
Chonetes sp.	1	3	1	2	2	1	2		
Schellwienella chemungensis		3	2	2	2	2	1		
Schuchertella chemungensis	1	4	1	4	2	1	5	1	1
Schizophoria "striatula"		1							
Rhipidomella pennsylvanica	3	3				1	2		
Dalmanella tioga	1					1	1		
D. leonensis			1			1			
Leptodesma sp.	6	7		1		1	2	1	2
Aviculopecten sp.		3	1	3	1	1	1		1
Other pelecypods	4	8	2	3	2	2	2	1	2
Syringospira alta		2	1	2	2	3	5		
"Lingula" sp.	1	4	2			1	2		
Gastropoda		4	1		1	2	3		
Bryozoa	5	9	1	3	1			1	
Crinoid columnals	4	16	1	6	1			1	
"Fish bone"	3	2		1				1	
Plant fragments	1	1	1	1	1	1	1		
Cyrtospirifer tionesta			3	12	4	1	3	2	
C. inermis		3		1	1	2	1		
C. warrenensis		12	1		3	1	3		
C. corriensis		4	1	3		2	3		
C. leboeufensis		1	1	1	2		3		
C. spicatus		3	1	3	3	3			
C. oleanensis		2							
"Spirifer" allegheniensis									

Oswayo shale. Quite expectedly, the cyrtospirifer abundant in that formation, *C. oleanensis,* is commonly associated with it.

The greatest increase in new species in this stage was among the pelecypod genera. Chadwick lists 81 new species from the Conewango, a figure very much greater than the 22 for the Canadaway, and 15 for the succeeding Cussewago Stage. Possibly many of these clams, like others of the late Paleozoic, preferred brackish waters. If so, it seems less likely that they immigrated from greatly distant faunal provinces, separated from the Appalachian geosyncline by wide stretches of ocean barrier. Perhaps the inference may be made that the expansion of the species of *Cyrtospirifer* in early

Conewango time was the result of factors other than new species arriving from remote faunal provinces.

Also arriving at this stage are considerable numbers of new gastropod species, including 10 species of *Platyceras*.

One significant fact brought out by the analysis tabulated above, is the intimate association of *Cyrtospirifer spicatus* and *C. leboeufensis* with each other, and also with a fauna including *Ambocoelia gregaria, Productella hirsuta, Chonetes scitulus, Schuchertella* sp., and *Rhipidomella pennsylvanica*—a group that observation has taught preferred the shale facies. Hence, a relationship of these forms to the shale lithofacies already inferred is supported by evidence from the biofacies.

Cyrtospirifer tionesta, postulated from a knowledge of its lithofacies as being a highly adaptable cyrtospirifer, is commonly found with any or all of the other species of its genus. With *C. oleanensis* it is found mainly in the Knapp conglomerate of the western locales, and with *C. warrenensis* it is almost always associated in the Salamanca formation. In general, however, a fossil bed will abound in a single species of *Cyrtospirifer*, as already observed for the Amity shale of the Corry vicinity.

Cussewago Stage

Of 20 collecting points in the Cussewago Stage, only 9 included cyrtospirifers. Of these, *C. oleanensis* (O) occurs in 6, *C. tionesta* (T) in 6, *C. lobatimusculus* (Lo) in 2, *C. corriensis* (Co) in 1 and *C. warrenensis* (Wa) in 1. *"Spirifer" allegheniensis* (Al) is present in 2.

Faunal associations are shown in the following table.

Discussion. Formations of the Cussewago Stage in general have fewer fossiliferous beds, to judge from the lesser number of collecting sites, and, in these, cyrtospirifers are less commonly found; only 43 per cent of the fossil lots provided cyrtospirifers.

The end of the Conewango Stage (and, according to Caster, 1934, of the Devonian System) saw the disappearance from among the brachiopods of the dalmanellids, the remaining *Atrypas, Rhipidomella pennsylvanica, Schizophoria "striatula," Productella arctirostrata, P. speciosa, P. lachrymosa, P. hirsuta, Camarotoechia sappho, Leiorhynchus multicosta, L. laura, Ambocoelia gregaria*, and *Athyris polita*. The most important new brachiopod arrivals are the generally abundant *Syringothyris randalli* and *S. angulata*, and two species of *Paraphorhynchus*. *Cyrtospirifer tionesta, C. oleanensis*, and *C. lobatimusculus* are not uncommonly found together, especially in the western locales; the other species of *Cyrtospirifer* were too seldom located to allow any good inferences to be made with regard to their mutual association. *C. oleanensis* and *C. tionesta* appear to have occupied the same ecologic niches with *Syringothyris angulata, Camarotoechia contracta, Productella lachrymosa, Ambocoelia gregaria, Spirifer asper* (?), *Chonetes scitulus, Rhipidomella pennsylvanica*, and possibly *Syringospira alta* and *Schuchertella chemungensis*. The other species are generally too few in numbers for any definite statements as to their biofacies to be made.

	X	O	T	Lo	Co	Wa	Al
Syringothyris texta			1				
S. randalli	1		1				
S. angulata	3	5	5	2	1	1	2
Camarotoechia contracta	2	5	3	2		1	1
Productella hirsuta			1				
P. lachrymosa	2	1	2			1	
Productella sp.	2						
Ambocoelia gregaria		1	1			1	
Spirifer asper (?)	2	1	1			1	
Syringospira alta			1				
Chonetes scitulus	4	4	3	2	1	1	1
Chonetes sp.	3	1	1	1			
Rhipidomella pennsylvanica	2	4	2	2	1		2
Rhipidomella sp.	2	1	1	1	1		
Dalmanella sp.	1	1	1				1
Schizophoria sp.		1	1	1			
Leptodesma sp.	1	2	1	1			
Other pelecypods	1						
Gastropoda	1	1	3			1	
"*Lingula*" sp.		2	1				
Bryozoa	2	1	1	1			2
Crinoid columnals	2	4	3	2		1	2
Schuchertella chemungensis	2	1	2			1	1
Cyrtospirifer oleanensis			3	2	1	1	1
C. tionesta		3		2	1	1	1
C. lobatimusculus		2	2		1		
C. corriensis		1	1	1			
C. warrenensis		1	1				
"*Spirifer*" *allegheniensis*		1	1				

Perhaps the carnivorous gastropods—8 new species also arrive in this stage—although not too commonly found, made serious inroads upon the cyrtospirifers, helping to account for their greatly decreased numbers, but this is the merest assumption.

Berea Stage

Of 8 collecting points in the Berea Stage, 6 have yielded cyrtospirifers. Of these *C. oleanensis* (O) occurs in 3, *C. tionesta* (T) in 3, *C. lobatimusculus* (Lo) in 2, and *C. warrenensis* (Wa) in 2. "*Spirifer*" *allegheniensis* (Al) occurs in only 1.

Faunal associations are shown in the following table.

Discussion. The most fossiliferous part of the Corry sandstone is the basal bed, which contains spiriferids and syringothyrids in great numbers and which persists over a wide area. It is not surprising, perhaps, that in 75 per cent of the Corry collecting sites this bed was located and found to contain cyrtospirifers. Except for the observation that here, too, *C. tionesta*

	X	O	T	Lo	Wa	Al
Syringothyris angulata	1	2	2	2	1	1
Syringospira sp.		1	1	1	1	
Chonetes scitulus	1	2	2	2	2	1
Chonetes sp.		1	1			
Schuchertella chemungensis	1	1	2	1	1	1
Camarotoechia contracta	2	2	1	2	1	
Rhipidomella pennsylvanica	1	1	1	1	1	
Dalmanella leonensis	1					
Rhynchospira scansa			1			
Paraphorhynchus sp.	1					
Aviculopecten sp.	2	1	1	1	1	1
Leptodesma sp.	1					
Other pelecypods	1		1			
Bryozoa			1			
Crinoid columnals		2	2	1	1	
"Fish bone"	1					
Gastropoda				1		
Cyrtospirifer oleanensis			2	1	1	
C. tionesta		2		1	1	
C. lobatimusculus		1	1		1	
C. warrenensis		1	1	1		
"Spirifer" allegheniensis						

appears with any or all of the other cyrtospirifers, the data are too few to permit any important conclusions as to the biofacies relationships to be drawn.

Meadville Stage

Of 12 collecting points in the Meadville Stage only 6 yielded cyrtospirifers. Of these, *C. tionesta* (T) occurs in 6 and *C. lobatimusculus* (Lo) in 2.

Faunal associations are shown in the following table.

Discussion. A fact not brought out very well by the above list of species is the much fewer fossiliferous beds in this part of the section. In 50 per cent of these, however, cyrtospirifers were still present, and of these the principal species appears to have been *C. tionesta*, by a 3:1 ratio. In many fossil beds, gastropods (mainly *Platyceras* spp.) in considerable numbers have been found with cyrtospirifers, in many cases apparently closely fastened to the shell of the latter.

To summarize, the biologic interrelationships on the Catskill Delta must have been extremely complex, to judge from the abundant and varied faunas generally found associated with the cyrtospirifers. If we add to these associates others poorly or not at all preserved—animals with few hard parts, predators from other ecologic zones, microscopic food and parasitic organisms, etc.—the complexity becomes infinite. However,

	X	T	Lo
Athyris sp.	1		
Camarotoechia contracta	2	1	
C. sappho (?)		1	
Productella rectispina		1	
P. speciosa		1	
P. hirsuta (?)		2	1
P. lachrymosa		1	
P. arctirostrata		1	
Chonetes scitulus	1	3	1
Chonetes sp.		1	1
Dalmanella sp.		1	
Schuchertella chemungensis (?)	1		
Leptodesma sp.	1		
Other pelecypods	1	1	1
"Fish bone"	1		
"*Lingula*" sp.	3		
Gastropoda	1	2	1
Bryozoa	1	3	
Crinoid columnals		3	
Cyrtospirifer tionesta			2
C. lobatimusculus		2	

evidence from the biofacies largely supports that derived from the lithofacies. Shale facies forms of *Cyrtospirifer* are found with "ceramophilic" associates, and those of the sandy facies with sand-loving faunas. In general, the various cyrtospirifers are not found together, a fact somewhat supporting the validity of their recognition as distinct species, and the probability that many of them inhabited separate ecologic niches.

EVOLUTION OF *CYRTOSPIRIFER*

PART A: PHYLOGENY

It seems only natural that among the numerous species of cyrtospirifers that thrived in great abundance on the Catskill Delta, some species should have had their origins locally. Likewise it would seem quite possible, in view of the great length of time involved in the formation of the delta, that others of these would have had their origins in remote faunal provinces and would arrive as species foreign to the Appalachian province.

The problem in this section is to distinguish between these two groups, and to reconstruct the phylogeny of the *Cyrtospirifer* tribe as represented in the Upper Devonian—Lower Mississippian strata of eastern America. A diagram of the phylogeny of the group, upon which the following discussion is based, is given in figure 5.

The ancestry of the *Cyrtospirifer* tribe is not known. The most likely assumption would seem to be that the progenitor was one of the completely costate spirifers, which, more likely than not, also dwelt upon the Catskill Delta. Paeckelmann, in his phyletic lineage of the Spiriferidae, considered *Cyrtospirifer* as derived from *Spinocyrtia* (1931, p. 58). While this is a possibility, the shape of the shell, distinctive surface ornamentation and great separation in time seem to offer cogent objections.

Cyrtospirifer chemungensis persisted relatively unchanged throughout much of Cayuta time, and then underwent notable variation in form. At approximately the same time these changes took place, *C. preshoensis, C. angusticardinalis, C. hornellensis,* and *C. whitneyi* make their first appearance. It has been inferred that, in view of their abrupt appearance, distinctive morphologies, and unique micro-ornament, these were migrants from other regions. *C. whitneyi,* if we consider its great abundance in the American West, is almost certainly not a form endemic to the Catskill Delta. The effect of this invasion upon the local cyrtospirifers was great.

C. preshoensis, which arrived somewhat earlier than the other exotic species, had a high, rounded fold, with a complementary wide, shallow sinus. These shell features were possessed, as well, by *C. altiplicus.* In other respects its shell is quite unlike *Cyrtospirifer altiplicus,* which is a very wide form with many lateral plicae, and short dental lamellae. The latter features, however, are very similar to those of *C. chemungensis. C. altiplicus,* therefore, is a species which apparently combines the characters of both the narrow form with the high fold, and the wide form with many costae. It is found exactly in that part of the stratigraphic section where such a hybrid could be expected. It is of quite large size and robust character, and occurs in great abundance within its geographic area. Hence, it may be postulated that we have here a hybrid cyrtospirifer, the result of inter-

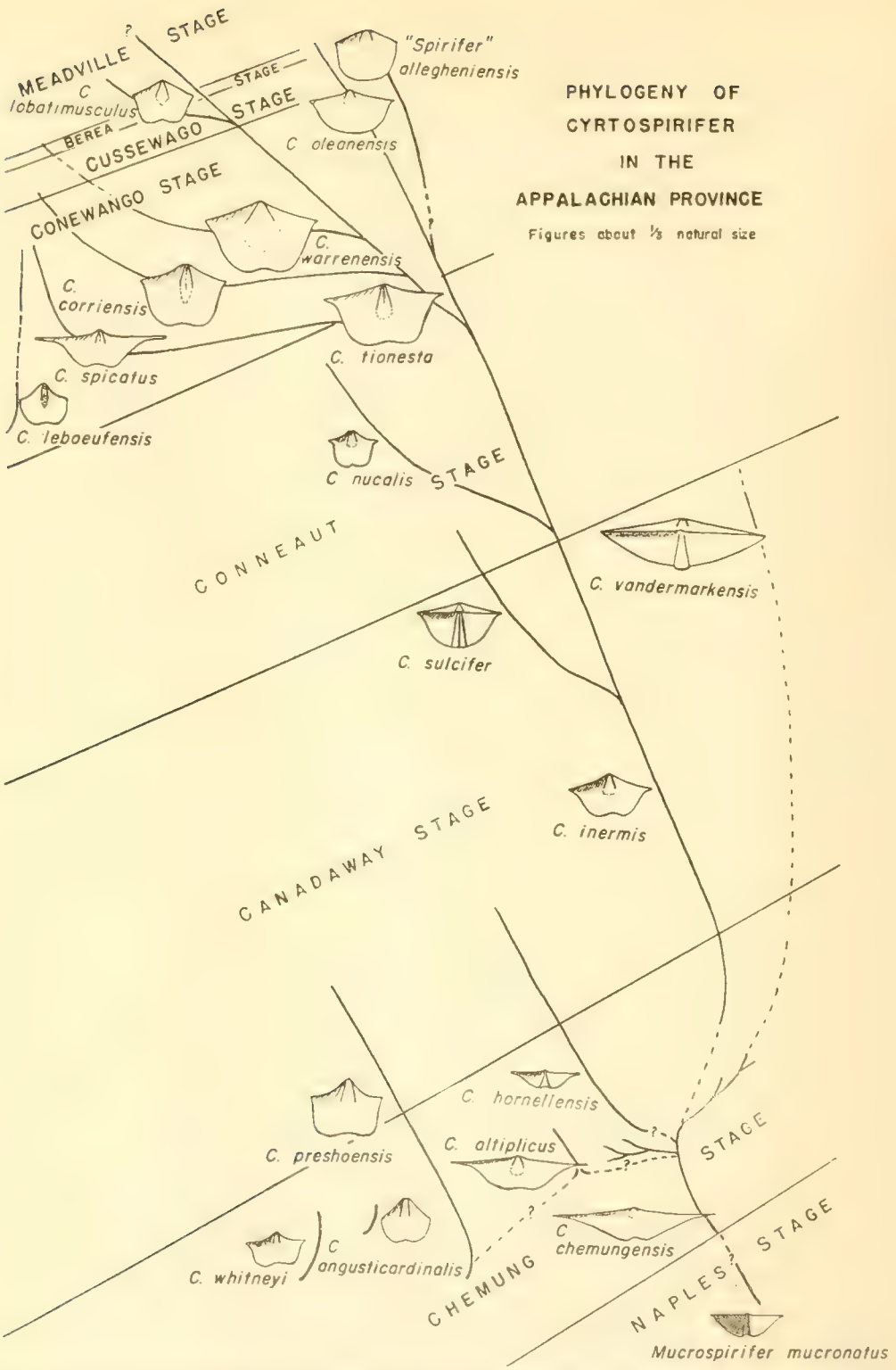


Fig. 5. Inferred phylogeny of the species of *Cyrtospirifer* in the Catskill Delta.

mixing of genes from two phyletic strains. The high fold and wide, shallow sinus may have been controlled by a single genetic mechanism.

C. angusticardinalis, presumed to be another exotic form, seems not to have been able to survive for long in the Chemung environment, possibly because of its preference for a muddy, near-shore environment, and inability to adapt to the "Chemung" type of sedimentation.

This is far from true for another cyrtospirifer arriving in the latter part of Cayuta (i.e., early Wiscoy) time. *C. inermis*, as we have seen, was a more adaptable cyrtospirifer than those preceding it. Its origin is more obscure, for it appears suddenly in early Wiscoy time, somewhat above the "zone of variation" wherein many varieties of *C. chemungensis* occur. Some of the latter, as shown in Plate 3, figures 4 and 5, rather resemble the later form. Hence, there are two main possibilities for its origin: the species may have been an off-shoot from a stock which had its habitation in regions other than the Appalachian province; or, it may have originated on the delta from previously existing cyrtospirifers, with or without introgression of genetic features from foreign species. Since it is of a form which has not been described from other areas (at least, not in the adequate manner that would make identification certain), and since there is some slight evidence of forms transitional to the earliest Chemung cyrtospirifer, the latter hypothesis is preferred. Its lack of the distinctive fine micro-ornament, possessed by most of the exotics of this time, offers some support for this.

Also arriving in early Wiscoy time was *C. hornellensis*. Since it has not been found in other regions, and somewhat resembles *C. inermis* in the number of lateral costae, dental lamellae, etc., it is tentatively considered to be of local origin, possibly an offshoot from one of the varieties of *C. chemungensis*. On the other hand, its distinctive micro-ornament bespeaks a foreign origin. Hence there is some question as to the exact derivation of this species.

The zone of postulated invasion by alien species is therefore an important one. New species appear both by apparent hybridization and by direct migration. Adaptive zones once occupied by *Cyrtospirifer chemungensis* were taken over by newly created and newly arriving forms. Unable to withstand the competition within its own ecologic niches from its own relatives, *C. chemungensis* vanished from the delta. Its disappearance has been inferred to be largely due to a biologic change in environment, although there may have been contributing changes in sedimentation and other aspects of the environment for which there is little evidence in the record.

But although *C. chemungensis* disappeared, a form somewhat resembling it, *C. vandermarkensis*, made a brief appearance late in the Canadaway Stage. From their somewhat similar shell shape—both are wide forms—their possession of numerous fine costae, beginning mainly at the hingeline, and of a very small, subcircular muscle scar, with very brief dental lamellae, it is thought the two are closely related. The long stratigraphic and time interval between them, however, is not easy to account for. One obvious

explanation would be that a stock similar to the early cyrtospirifer had lingered in areas remote from the Catskill Delta, making a brief, probably final, appearance, albeit in somewhat altered form, at the time of deposition of the rocks in which *C. vandermarkensis* is now found.

The part played by *Cyrtospirifer inermis* in the further evolution of the the clan is believed to be an extremely important one. From its basic stock, in the Canadaway Stage, *C. sulcifer* evolved, possibly in a somewhat isolated geographic and biologic adaptive niche. The morphologic changes needed to create this species were mainly the development of a median groove in the brachial valve. In early Conneaut time, a second descendant, *C. nucalis*, appeared. This is a small, obese form, probably adapted to a specialized environment in the delta. In the late Conneaut or early Conewango Stage, the somewhat similar and very adaptable *C. tionesta* is thought to be derived from the basic stock of *C. inermis*. The very important role played by this species, itself an ancestral stock, will be discussed shortly.

Also related to the ancestral stock of *C. inermis* is *C. oleanensis*. Many shell features point to this relationship—the general shell shape, the narrow, rounded costae, the longitudinally striate, subcordate muscle scar, etc.—but its distinctive specific characteristics, notably the prominent dorsal muscle scar and large hingeplate, are newly evolved. The phenomenal expansion of *C. oleanensis* in the Oswayo formation, after a limited occurrence throughout the entire lower part of the Conewango Stage, possibly indicates a gradual adaptation to a particular ecologic niche, with expansion as that "adaptive zone" greatly broadened late in the stage. As some slight support for this view, it is noted that *C. tionesta, C. warrenensis*, and possibly *C. corriensis*,—possible competitors with this species in the time of its scarcity—are not present in the Oswayo of the Olean area, where *C. oleanensis* is so abundant.

Finally, "*Spirifer*" *allegheniensis* Caster may be descended from *C. inermis*. The undoubted presence in this species of a delthyrial plate, together with the other diagnostic features required of the genus, would seem to indicate congeneric relationship of this form with *Cyrtospirifer*. The longitudinally striate muscle scar, thickly callused umbonal region, slight median ridge in the brachial valve, and fairly well-defined sinus (all shown in figs. 7 to 11, Pl. 9) point to *C. inermis* as its probable ancestor. The semicircular shell, fewer and bifurcating lateral costae are quite distinctive specific differences, however. Since this species has not been reported from other faunal regions, we may presume that it originated in the Appalachian province.

Thus we have the "Ahnenreihe," or ancestral series, represented by *C. inermis*, giving rise to a "Stufenreihe, or step series, consisting of five related but distinct species of *Cyrtospirifer* (Abel, 1939, *in* Simpson, 1953, p. 220).

Until found in and described from remoter regions, *C. tionesta* is considered to be a species endemic to the Appalachian province, evolved from

its most obvious ancestor, *C. inermis*, in late Conneaut or early Conewango time.

In Amity time, just after the appearance of *C. tionesta*, the great expansion of the cyrtospiriferid group took place. *C. tionesta* is believed, from the available evidence, to have been the ancestral series from which a new step series evolved. The lower stratigraphic range of *C. tionesta*, alone among the later cyrtospirifers, overlaps that of *C. inermis*, hence there exists a relationship between the two in time. The geographic range of *C. tionesta* extends farther east than does that of any of the post-Conneaut cyrtospirifers; there is therefore an intimate relationship in space. Finally, in general size and shape, height of cardinal area, approximately equivalent numbers of lateral costae, and divergence of the dental lamellae, the two species have relationships in morphology.

By evolving highly adaptive, spike-like extensions to the hingeline, the mud- and silt-dwelling form, *C. spicatus*, emerged as a species separate from *C. tionesta*. From its retention of shell characteristics similar to the parental stock—broad costae, with fine growth lines, a round-sided sulcus, and a not dissimilar muscle scar and dental lamellae—the ancestry of this form has been inferred.

Another likely offshoot from the ancestral series of *C. tionesta* was *Cyrtospirifer warrenensis*. A large form with widely divergent dental lamellae and a broad muscle scar, it yet possesses the broad ribs and rounded sinus margins of its progenitor. Its general occurrence in sandstone beds of predominantly shale sections points to a probable habitation in an ecologic niche of its own.

C. corriensis also probably had its origin in the parental stock of *C. tionesta*. The broad costae, high fold and shallowly rounded sinus are similar to the latter, but the dental lamellae have lengthened and converged, while the shell has become more gibbous and narrower.

C. lobatimusculus also may be considered part of the "Stufenreihe" of *C. tionesta* with some degree of certainty, for it retains the broad costae, gently rounded sulcus and high fold of that form, but develops a uniquely lobed muscle and a smaller, rather distinctive shell form.

Thus a second ancestral series, *C. tionesta*, has given rise to another step series, consisting of four closely related cyrtospirifer species.

Perhaps it may be theorized that the rapid evolution and speciation near the upper limit of the range of *C. inermis* was due to the use of a large store of potential genetic variability existing in that species (Wright, Sewall, 1945, *in* Simpson, G. G., 1953, p. 77). Much phenotypic variability certainly existed in *C. inermis* throughout its range. However, this is mere speculation, for which there is no evidence one way or the other.

Appearing in early Conewango time with some of the above we have already noted *C. leboeufensis*. This shell is of a shape quite distinct from any belonging to the "Stufenreihe" *C. spicatus—C. lobatimusculus*, and from any of the varieties of the ancestral *C. tionesta*. As noted under the de-

scription of this species, it has a shell form unlike any other cyrtospirifer in its zone, a uniquely striate muscle scar, and a smoothly costate surface. For these reasons it is considered to be an exotic migrant from some other faunal province.

PART B: EVOLUTIONARY TRENDS

It might be next inquired whether any clear-cut trends in shell morphology are illustrated by the cyrtospirifers.

In shell shape, the attenuate, wide forms of this genus appear earliest, although *C. spicatus* of the Conewango Stage also develops greatly extended extremities to the hingeline, probably as an adaptation to its environment.

In size of shell, we have noted that the largest shells are generally merely an intraspecific adaptation to environment. The smallest species, *C. hornellensis,* predominates in the Wiscoy shale facies, while the next smallest, *C. nucalis,* from the Conneaut Stage, has probably developed its size as a response to environmental pressure. If, however, the general size trend be considered, the largest species appear relatively late, in Conewango time; *C. tionesta* and *C. warrenensis* are examples. This size increase is in keeping with Newell's views, that increasing robustness in higher stratigraphic levels takes place in the lower taxonomic groups (1949, p. 110).

In costation, the cyrtospirifers with numerous fine costae, beginning (mainly) at the hingeline are found in the early stages. The most common number of lateral ribs for the group, starting in the mid-Chemung (if not earlier) appears to be about 24. Costation in the sinus and fold, however, seems to show a tendency to increase. *C. chemungensis,* the earliest form, has few costae on these parts, while *C. tionesta* and members of its series generally display many; the trend is certainly not well-defined, however. *C. preshoensis,* for instance, is an early species, yet has abundant bifurcation in the sinus, creating many fine costae. *C. warrenensis,* appearing late, has a minimal amount of bifurcation, as does the species appearing latest of all, *C. lobatimusculus.*

The three species with distinctive micro-ornament all appear in the Chemung Stage.

In broadness of the costae, again, the feature is one which develops relatively late in the history of the group.

The radiately striate, and larger, muscle scar seems to come late, in post-Conneaut time, in the *Cyrtospirifer* group. The rather distinctive, slender adductor muscle scar, too, appears late in the evolution of the cyrtospirifers.

Perhaps the most significant evolutionary adaptation is that already noted especially in *C. inermis* and *C. tionesta,* wherein a size and shape of shell is achieved which, in the spiriferids, harmonized best with the "Chemung" environment, and remains relatively static for long periods of time; a form which yet possesses an adaptive flexibility which is able to cope with new conditions as they appear. This seems to be true as well of many other of the more successful spirifer genera.

CONCLUSIONS

The tribe of "*Spirifer disjunctus*" in the Appalachian province has proved to be a complex of generally closely related species, united by their possession of morphologic features common to the genus, but generally easily distinguishable by other features possessed only by the individual species. These species have well-defined ranges of variable duration in the Upper Devonian-Lower Mississippian strata of eastern North America. A close relationship has been shown to exist, in some, between shell morphology and the sedimentary and biologic environment.

The phylogeny of the cyrtospirifers in the Catskill Delta has been seen to consist of two principal lines of closely related taxonomic groups, together with other species, which, from their anatomical characteristics and other evidence, are found to be immigrants from other shores.

It has been shown that the amount of speciation and the abundance of individuals in a group of spiriferids approaches an inverse relationship.

Finally, the value of a rapidly evolving group of organisms may be comparable to that of whole assemblages of fossils, as stratigraphic indices.

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PLATE 1

Cyrtospirifer chemungensis (Conrad); *Cyrtospirifer altiplicus* n. sp.

Cyrtospirifer chemungensis (Conrad) . . . p. 18

Fig. 1. Plastoplesiotype. Interior of pedicle valve, showing brief dental lamellae, and embedded subcordate muscle scar. Y.P.M. 19328. Cayuta formation. ½ mile south of Nelson, Pa.

2. Plastoplesiotype. Brachial exterior. Y.P.M. 19329. Cayuta formation, lower part. Highway 2 miles north of Owego, N.Y.

3. Plastoplesiotype. Brachial valve interior. Y.P.M. 19331. Cayuta formation. Glory Hill, Waverly, N.Y.

4. Plastoplesiotype. Interior of pedicle valve of young individual, showing less calcitic secondary growth than that in figure 1. Y.P.M. 19333. Cayuta formation. Highway ½ mile south of West Addison, N.Y.

5. Plesiotype. Posterior view of a pedicle valve. Y.P.M. 19334. Cayuta formation, lower part. Highway 2 miles north of Owego, N.Y.

6. Plastoplesiotype. Pedicle valve showing fine costae which begin at the hingeline. Y.P.M. 19336. Cayuta formation. Glory Hill, Waverly, N.Y.

7. Plastoplesiotype. Pedicle valve interior. Y.P.M. 19338. Cayuta formation, lower part. Highway 2 miles north of Owego, N.Y.

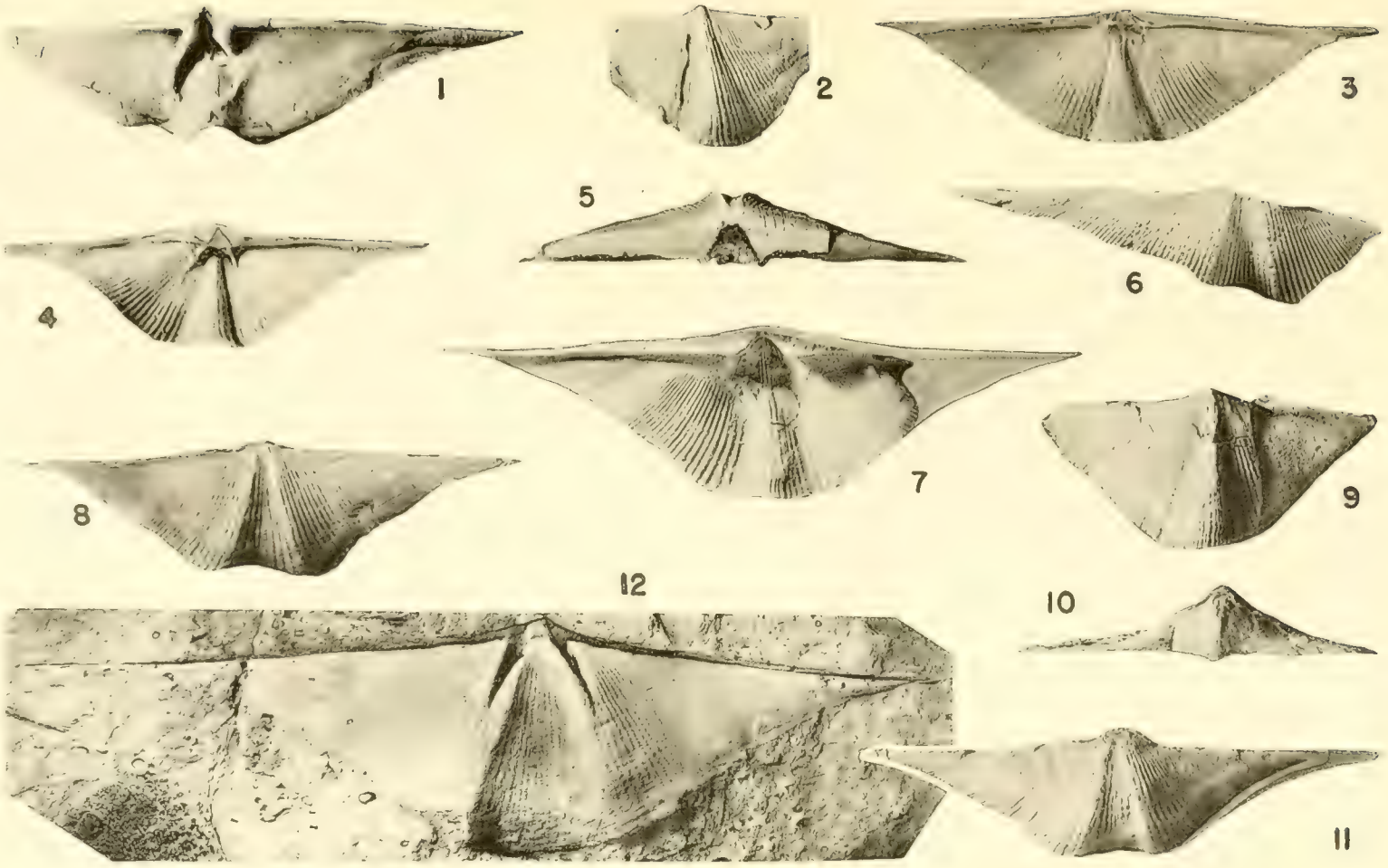
8. Plastoplesiotype. Pedicle valve exterior. Y.P.M. 19340. Lower part of the Cayuta formation. Highway 2 miles north of Owego, N.Y.

Cyrtospirifer altiplicus n. sp. . . . p. 20

9, 10. Paratype. Part of a brachial valve; posterior view of same to show high fold. Y.P.M. 19341. Cayuta formation. Ryers Creek, near Lindley, N.Y.

11. Paratype. Pedicle valve showing incipient tripartition in lateral costae. Y.P.M. 19342. Cayuta formation. Ryers Creek near Lindley, N.Y.

12. Holotype. Natural cast of the pedicle valve of a large, mucronate specimen. Y.P.M. 19343. Cayuta formation. Sabinsville R.R. Station, Pa. (Coll. E. I. Leith, 1931.)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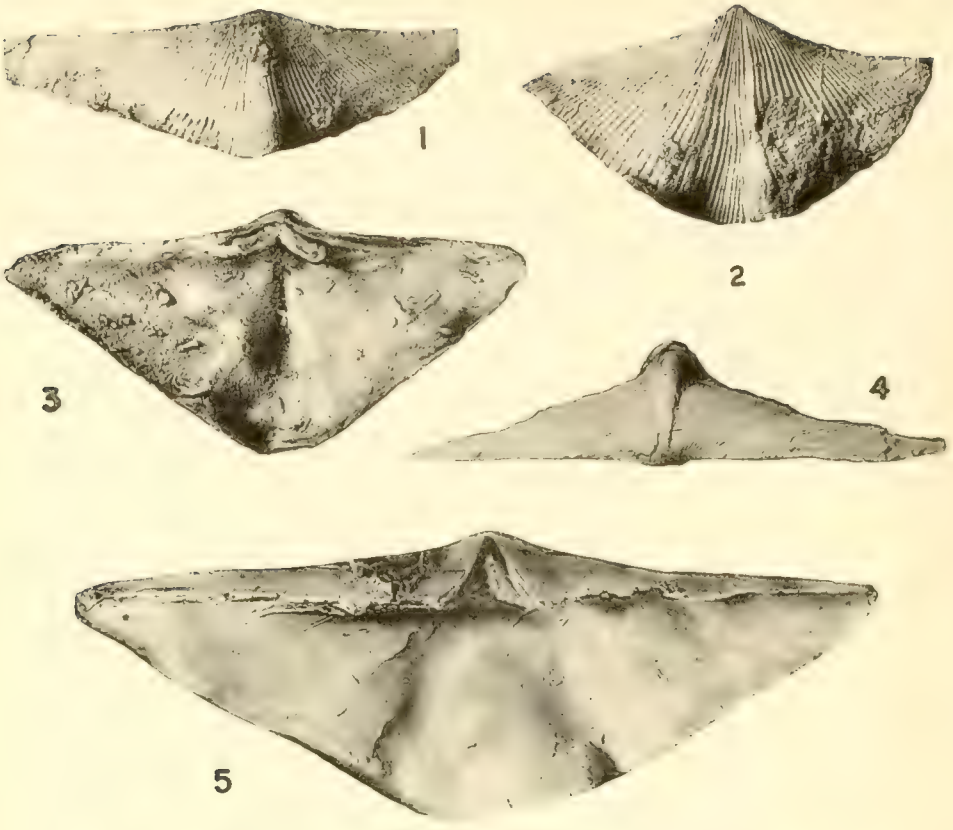
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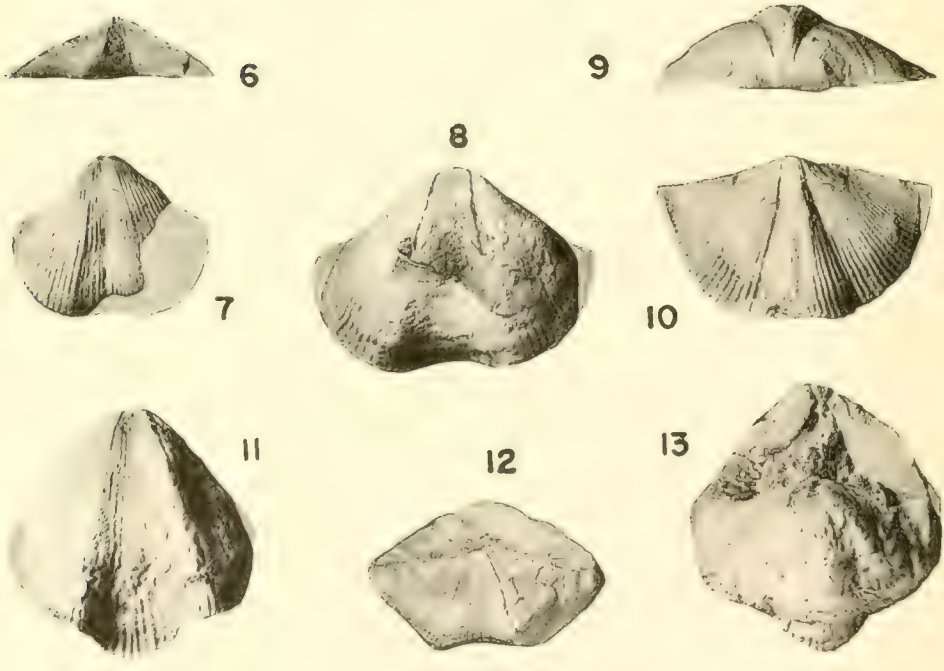
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PLATE 2

Cyrtospirifer altiplicus n. sp.; *Cyrtospirifer angusticardinalis* n. sp.

Cyrtospirifer altiplicus n. sp. . . . p. 20

Fig. 1. Plastoparatype. Latex impression of part of brachial valve, showing the fold and fine costae beginning at the hinge-line. Y.P.M. 19345. Cayuta formation. Sabinsville R.R. Station, Pa. (Coll. E. I. Leith, 1931.)

2. Plastoparatype. Latex impression of part of pedicle valve, showing the sinus. Y.P.M. 19347. Cayuta formation. Sabinsville R.R. Station, Pa. (Coll. E. I. Leith, 1931.)

3. Plastoparatype. Latex impression of interior of a brachial valve, showing tooth sockets and stout hingeplate. Y.P.M. 19349. Cayuta formation, Ryers Creek, near Lindley, N.Y.

4. Paratype. Posterior view of a brachial valve, showing high, rounded fold. Y.P.M. 19350. Cayuta formation. ½ mile south of Sabinsville, Pa.

5. Plastoparatype. Latex impression of a large pedicle valve, showing high cardinal area, and broad sinus. Y.P.M. 19352. Cayuta formation, Sabinsville R.R. Station, Pa. (Coll. E. I. Leith, 1931.)

Cyrtospirifer angusticardinalis n. sp. . . . p. 21

6. Paratype. Posterior view of pedicle valve, showing cardinal area and delthyrium. Y.P.M. 19353. Cayuta formation, just below base of Wiscoy formation. Morgan Creek, Lindley, N.Y.

7. Plastoparatype. Typical pedicle valve. Y.P.M. 19355. Cayuta formation. Morgan Creek, Lindley, N.Y.

8. Paratype. Another pedicle valve, showing trace of the dental lamellae. Y.P.M. 19356. Cayuta formation. Morgan Creek, Lindley, N.Y.

9, 10. Paratype. Posterior and dorsal aspects of a brachial valve. Y.P.M. 19357. Cayuta formation, Morgan Creek, Lindley, N.Y.

11, 12, 13. Holotype. Ventral, posterior, and dorsal views of a geron-tic individual, showing very high, almost flat, cardinal area. Y.P.M. 19358. Cayuta formation. Morgan Creek, Lindley, N.Y.

PLATE 3

Cyrtospirifer chemungensis n. sp.; *Cyrtospirifer preshoensis* n. sp.

Cyrtospirifer chemungensis n. sp. (variants) . . . p. 18

Fig. 1. Plastoplesiotype. Brachial interior. A small variety of *C. chemungensis* with fewer and coarser ribs. Y.P.M. 19360. Wellsburg formation. Ashley Hill, Elmira, N.Y.

2. Plastoplesiotype. Dorsal view of a brachial valve; a variety similar to figure 1. Y.P.M. 19362. Wellsburg formation. Ashley Hill, Elmira, N.Y.

3. Plastoplesiotype. A variety with a sigmoidal lateral commissure and attenuate extremities. Y.P.M. 19364. Cayuta formation. Glory Hill, 2 miles west of Waverly, N.Y.

4, 5. Plastoplesiotypes. Exterior and interior of a pedicle valve. A variety with fewer lateral costae and narrower than typical *C. chemungensis*, but with similar brief dental lamellae. Y.P.M. 19366, 19368. Upper part of Cayuta formation. Highway west of South Addison, N.Y.

6. Plastoplesiotype. Pedicle valve interior; another attenuate variety with prominent teeth. Y.P.M. 19370. Upper part of Cayuta formation. Glory Hill, Waverly, N.Y.

Cyrtospirifer preshoensis n. sp. . . . p. 22

7. Paratype. Pedicle and brachial valves of average size and shape, embedded in sandstone matrix. Y.P.M. 19371. Cayuta formation, upper part. Ryers Creek, Lindley, N.Y.

8. Plastoparatype. Brachial valve interior, showing long, narrow dental sockets, and broad, thin crural plates (the one on the left partly missing). Y.P.M. 19373. Cayuta formation, upper part. Lindley, N.Y.

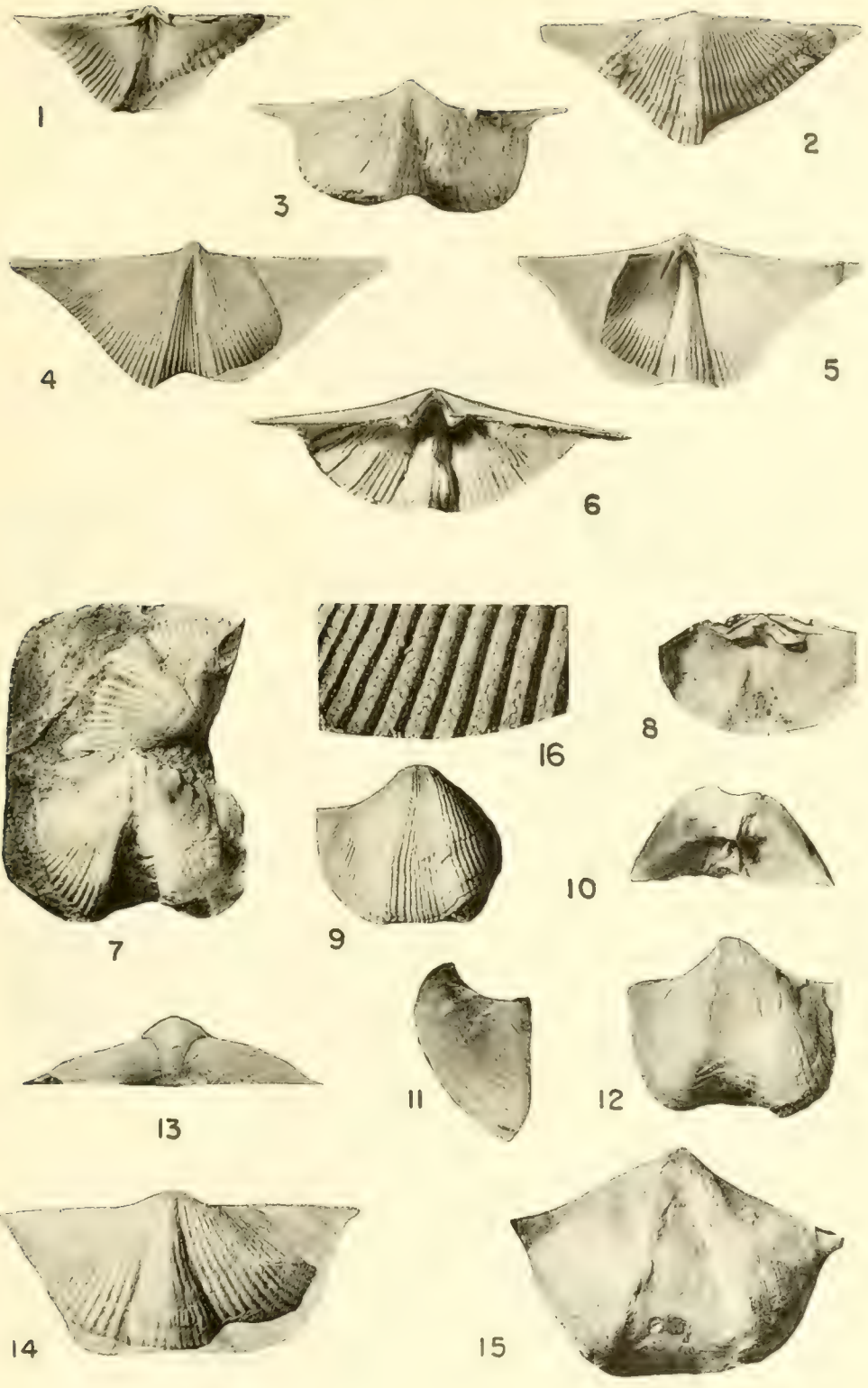
9. Plastoparatype. Part of pedicle valve exterior, showing bifurcation on sinus. Y.P.M. 19375. Cayuta formation, Ryers Creek, Lindley, N.Y.

10, 11, 12. Holotype. Posterior, side, and ventral views of a typical pedicle valve. Y.P.M. 19376. Cayuta formation, upper part. Ryers Creek, Lindley, N.Y.

13, 14. Paratype. Posterior and dorsal aspects of a large brachial valve, showing rather high, rounded fold. Y.P.M. 19377. Cayuta formation, upper part. Ryers Creek, Lindley, N.Y.

15. Paratype. Pedicle valve of large individual, showing typical, shallow, broad sinus. Y.P.M. 19378. Cayuta formation, upper part. Ryers Creek, Lindley, N.Y.

16. Paratype. Enlargement (x6) of costae, showing fine, overlapping, spinose micro-ornament. Y.P.M. 19379. Cayuta formation, upper part. Ryers Creek, Lindley, N.Y.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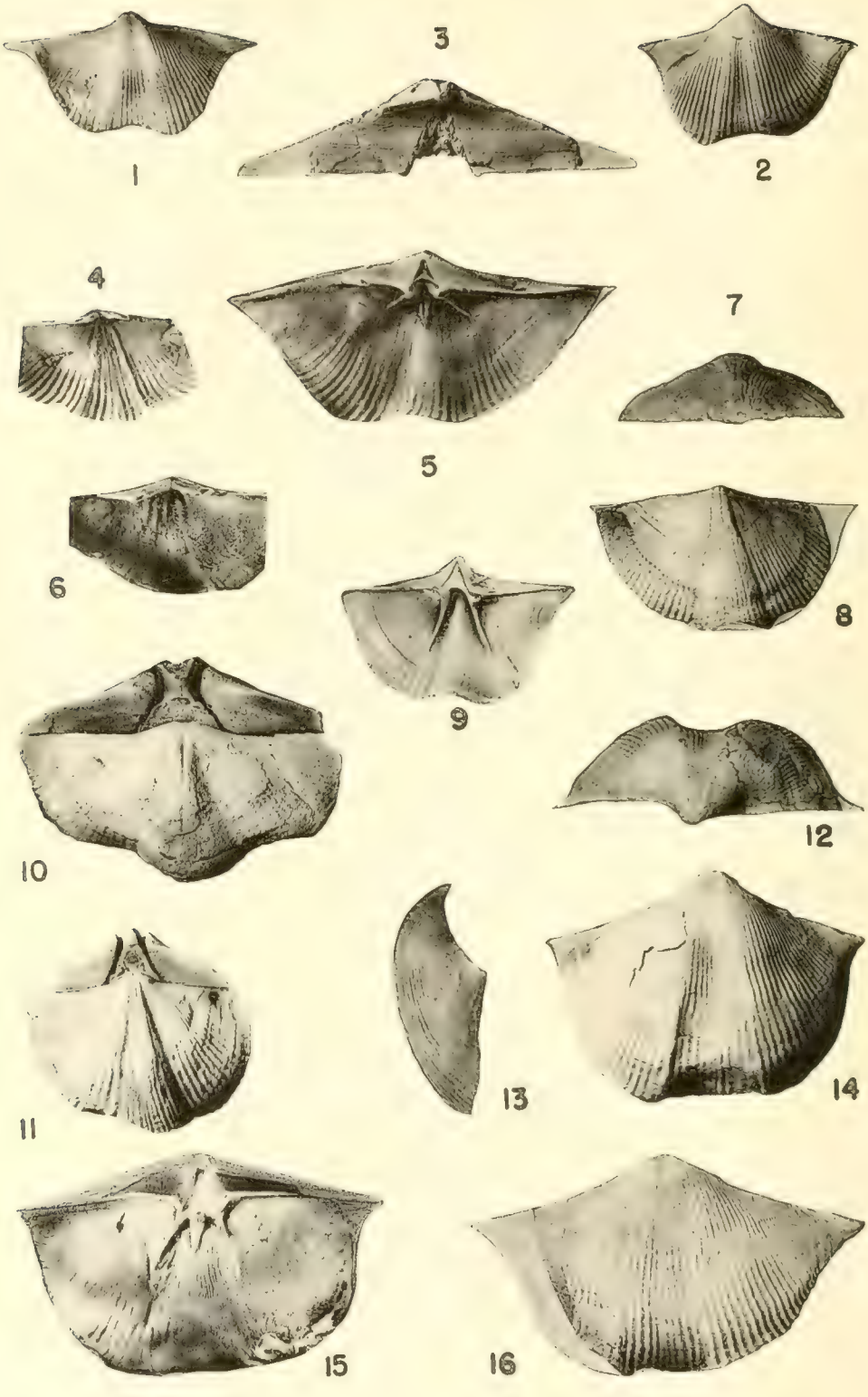
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PLATE 4

Cyrtospirifer inermis (Hall) . . . p. 24

Fig. 1. Plastoplesiotype. Pedicle valve of average-sized individual, showing bifurcation in sinus. Y.P.M. 19381. Ellicott shale. ½ mile south of Celoron, N.Y.

2. Plastoplesiotype. Another pedicle valve, with bifurcation in sinus contrasting with that shown in figure 1. Y.P.M. 19383. Volusia shale. Stream bed 2 miles south of Ischua, N.Y.

3. Plesiotype. Typical cardinal area. Y.P.M. 19384. Rushford sandstone. Rock Creek, Greenwood, N.Y.

4. Plastoplesiotype. Part of brachial valve interior, showing dental sockets. Y.P.M. 19386. "Chadakoin" formation. ½ mile south of Humphrey, N.Y.

5. Plastoplesiotype. Pedicle valve interior, illustrating an extreme in divergence of dental lamellae. Y.P.M. 19388. "Chadakoin" formation, upper part. 1 mile east of Bozard Hill, near Olean, N.Y.

6. Plastoplesiotype. Part of a brachial valve, showing muscle scar and dental sockets. Y.P.M. 19390. "Chadakoin" formation, upper part. 1 mile east of Bozard Hill, near Olean, N.Y.

7, 8. Plesiotype. Posterior and dorsal views of a brachial valve, showing low fold. Y.P.M. 19391. Volusia formation, upper part. Smith Hollow, Wellsville, N.Y.

9. Plastoplesiotype. Pedicle valve interior of an average-sized individual. Y.P.M. 19393. "Chadakoin" formation. Creek southeast of Salamanca, N.Y.

10. Plesiotype. Dorsal view of a natural cast, showing slender median ridge. Y.P.M. 19394. Ellicott shale. ½ mile south of Blockville, N.Y.

11. Plesiotype. Another natural cast from the same bed as that in figure 10, to show variation in size and shape. Y.P.M. 19395. Ellicott shale. ½ mile south of Blockville, N.Y.

12, 13, 14. Plesiotype. Posterior, side, and ventral views of pedicle valve of a large variety. Y.P.M. 19396. Canaseraga sandstone, upper part. Stephens Creek, Hornell, N.Y.

15. Plastoplesiotype. Pedicle valve interior, showing longitudinally striate muscle scar and delthyrial plate. Y.P.M. 19398. Caneadea formation. Fisher Hollow, Greenwood, N.Y.

16. Plesiotype. Pedicle valve of large individual. Y.P.M. 19399. Rushford sandstone. Christian Hollow, Greenwood, N.Y.

PLATE 5

Cyrtospirifer sulcifer (Hall) . . . p. 26

Fig. 1. Plesiotype. Exterior of a typical brachial valve, showing median groove on fold. Y.P.M. 19400. Cuba sandstone. Jersey Hollow, near Cattaraugus, N.Y.

2. Plesiotype. Pedicle valve. Y.P.M. 19401. Cuba sandstone. Jersey Hollow, near Cattaraugus, N.Y.

3. Plastoplesiotype. Ventral aspect of a typical pedicle valve. Y.P.M. Cuba sandstone. Jersey Hollow, near Cattaraugus, N.Y.

4. Plastoplesiotype. Brachial valve of a small, flat, mucronate variety found in the shale facies. Y.P.M. 19405. Volusia formation. Redwater Creek, southwest of Wellsville, N.Y.

5. Plastoplesiotype. Pedicle valve interior, in which a median groove is present in the sinus. Y.P.M. 19407. Volusia formation. 1 mile northwest of Hinsdale, N.Y.

6. Plastoplesiotype. Brachial valve interior, showing tooth sockets. Y.P.M. 19409. Volusia formation. 1 mile northwest of Hinsdale, N.Y.

7. Plesiotype. Pedicle valve exterior. Y.P.M. 19410. Cuba sandstone. Quarry ½ mile south of Cattaraugus, N.Y.

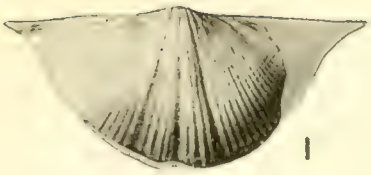
8. Plastoplesiotype. Muscle scar in the pedicle valve of a large individual. Y.P.M. 19412. Cuba sandstone, Cuba Lake, N.Y. (Coll. C. O. Dunbar and P. Sartenaer, 1953.)

9. Plastoplesiotype. Brachial valve interior, showing dental sockets and muscle scar. Y.P.M. 19414. Volusia formation. Redwater Creek, southwest of Wellsville, N.Y.

10. Plastoplesiotype. Brachial valve exterior. Y.P.M. 19416. Machias formation, just below base of Cuba sandstone. Cuba Lake, N.Y.

11. Plesiotypes. Two natural casts of brachial valves embedded in sandstone matrix. Y.P.M. 19417. Machias formation. Cuba Lake, N.Y.

12, 13. Plesiotype. Cardinal area and ventral view of a very large, subquadrate individual, common in the Cuba sandstone. Y.P.M. 19418. Cuba sandstone. Munger Hollow, Cuba Lake, N.Y.



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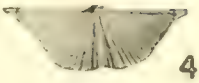

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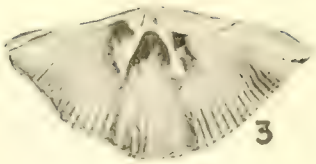

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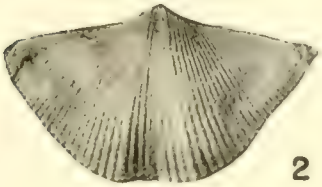

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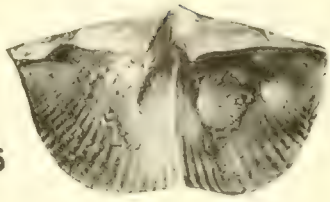

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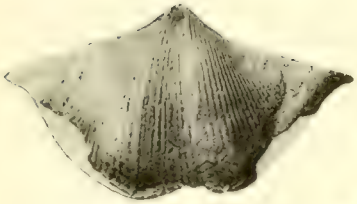

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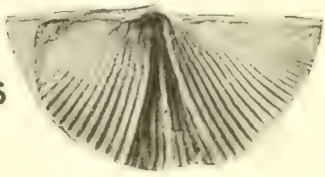

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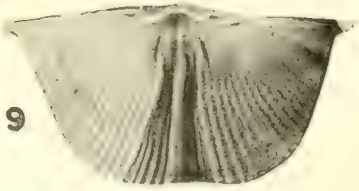

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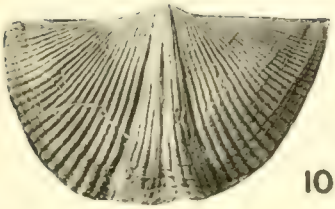

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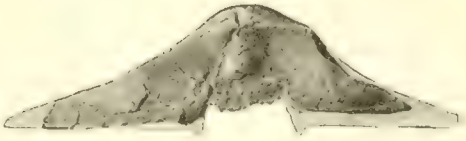

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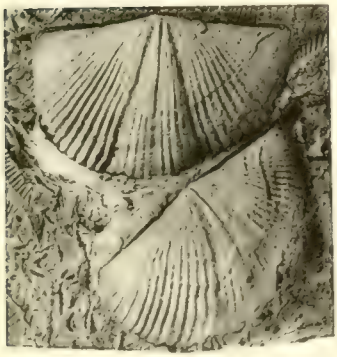

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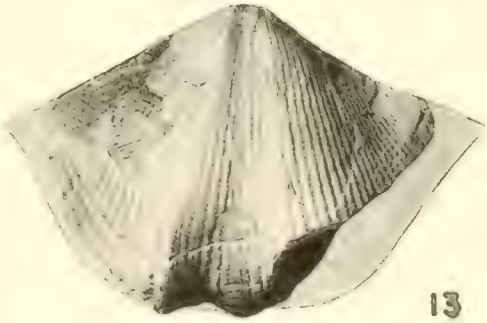

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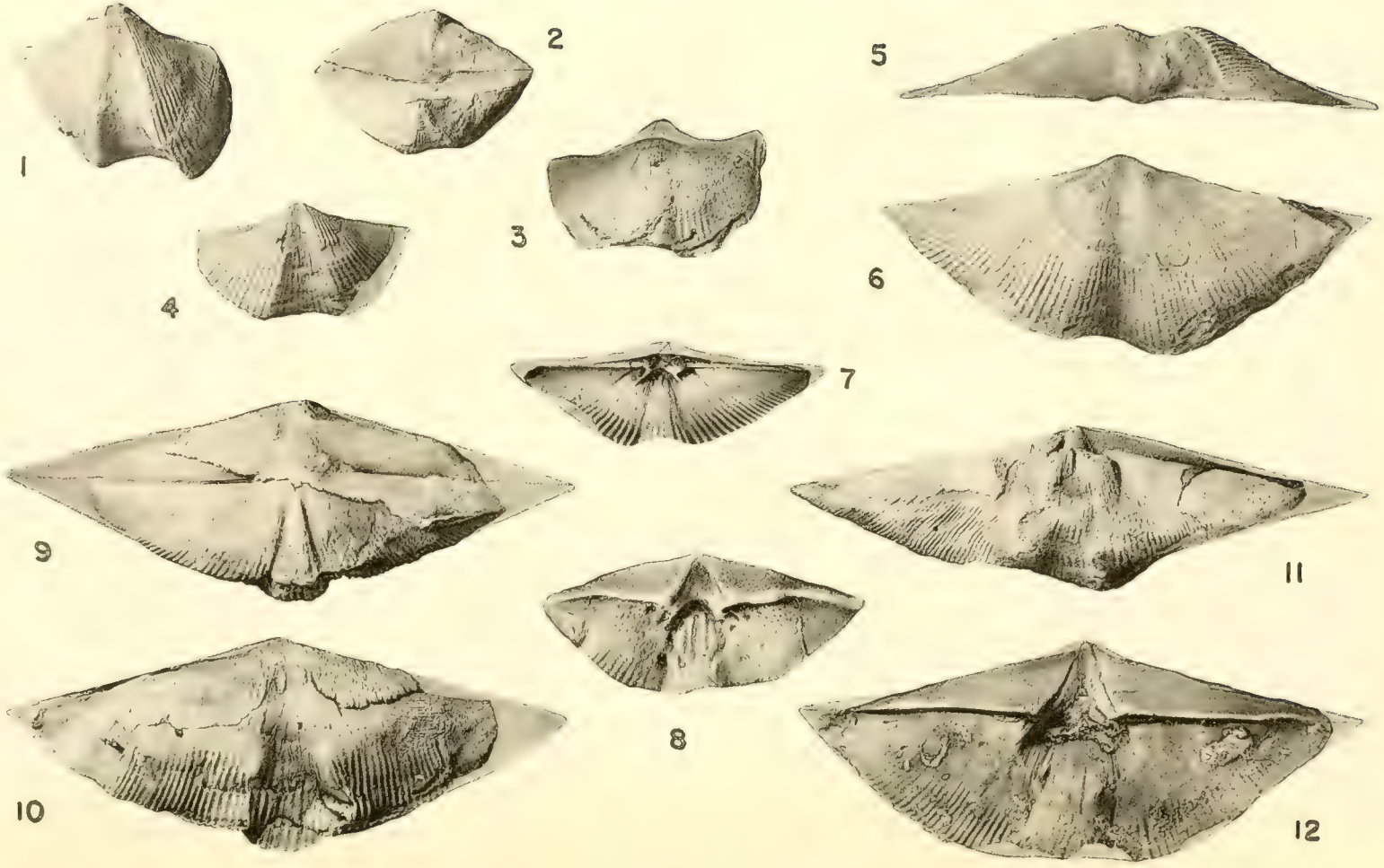
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PLATE 6

Cyrtospirifer whitneyi (Hall); *Cyrtospirifer sulcifer* (Hall); *Cyrtospirifer vandermarkensis* n. sp.

Cyrtospirifer whitneyi (Hall)

Fig. 1. Homotype. Ventral view of a distorted specimen. Y.P.M. 19419. Highpoint formation, just below base of Wiscoy, in shale. Glendening Creek, 3 miles southwest of Addison, N.Y.

2, 3. Homotype. Posterior and dorsal views of another distorted specimen. Y.P.M. 19420. From same bed as specimen shown in figure 1.

4. Homotype. Ventral view of pedicle valve, with trace of dental lamella on the left showing slightly. Y.P.M. 19421. Wiscoy formation. Stephens Creek, Hornell, N.Y.

Cyrtospirifer sulcifer (Hall) . . . p. 26

5, 6. Plesiotype. Posterior and ventral views of a pedicle valve of a large variety found in the Cuba sandstone. Y.P.M. 19422. Munger Hollow, Cuba Lake, N.Y.

Cyrtospirifer vandermarkensis n. sp. . . . p. 27

7. Plastoparatype. Pedicle valve interior of a young individual, showing restricted, widely divergent dental lamellae. Y.P.M. 19424. Machias formation, just below base of Cuba sandstone, ½ mile west of Franklinville, N.Y.

8. Plastoparatype. Interior of another pedicle valve, from an old individual, showing deeply embedded, subcordate muscle scar, brief dental lamellae, and closure of delthyrium by secondary shell growth. (and delthyrial plate). Y.P.M. 19426. Same bed as above.

9, 10. Holotype. Dorsal and ventral aspects of a partially exfoliated specimen showing rounded lateral commissure, high area, and well-defined fold. Y.P.M. 19427. Machias formation from a sandstone bed about 50 feet below top of the formation. Vandermark Creek, near Scio, N.Y.

11. Paratype. Pedicle valve exterior, showing fine costae beginning at the hingeline. Y.P.M. 19428. Same faunule as above.

12. Plastoparatype. Pedicle valve interior, showing typically broad cardinal area and restricted dental lamellae. Y.P.M. 19430. Some faunule as above.

PLATE 7

Cyrtospirifer hornellensis n. sp.; *Cyrtospirifer nucalis* n. sp.

Cyrtospirifer hornellensis n. sp. . . . p. 28

Figs. 1, 2, 3. Holotype. Posterior, ventral, and side views of a pedicle valve. Figure 2 shows trace of dental lamellae. Y.P.M. 19431. Wiscoy shale, upper part. Hammer Creek, near Hornell, N.Y.

4. Paratype. Brachial valve, showing typical fold, increasing in width toward the front. Y.P.M. 19432. Same faunule as above.

5. Plastoparatype. Pedicle valve. Y.P.M. 19434. Canaseraga sandstone, lower part. Stephens Creek, Hornell, N.Y.

6. Paratype. Two brachial valves embedded in siltstone matrix; at right, a larger, presumably gerontic, individual. Y.P.M. 19435. Canaseraga formation. Stephens Creek, Hornell, N.Y.

7. Paratype. Enlargement (x8) to show fine, spinose microornament. Y.P.M. 19437. Wiscoy formation. Stephens Creek, Hornell, N.Y.

Cyrtospirifer nucalis n. sp. . . . p. 29

Figs. 8, 9. Plastoholotype. Ventral and side views of a typical pedicle valve. Y.P.M. 19439. "Chadakoin" formation, lower part. Highway ½ mile east of Carrollton, N.Y.

10, 18. Plastoparatype. Ventral and posterior views of pedicle valve of another specimen, the latter showing typical V-shaped sinus. Y.P.M. 19441. Volusia formation. 1 mile east of Franklinville, N.Y.

11, 12. Paratype. Cardinal and ventral view of (partial) pedicle valve. Y.P.M. 19442. "Chadakoin" formation. Jersey Hollow, near Cattaraugus, N.Y.

13. Paratype. Dorsal view of a brachial valve. Y.P.M. 19443. "Chadakoin" formation, Jersey Hollow, near Cattaraugus, N.Y.

14. Paratype. Another brachial valve of typical shape. Y.P.M. 19444. Same faunule as specimen in figure 12.

15, 20. Plastoparatype. Brachial valve interior; figure 20 enlarged (x2) to show dental sockets. Y.P.M. 19446. "Chadakoin" formation, lower part. Highway ½ mile east of Carrollton, N.Y.

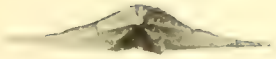
16. Plastoparatype. Pedicle valve interior, showing secondary calcification closing delthyrium. Y.P.M. 19448. "Chadakoin" formation, lower part. Highway just east of Ceres, N.Y.

17. Plastoparatype. Another pedicle valve interior. Y.P.M. 19450. Same faunule as the above.

19. Plastoparatype. Pedicle valve interior (x2). This specimen, and those in figures 16 and 17, form a series showing progressive calcification of the pedicle opening as secondary material forms, joins along a suture, and, as in figure 16, finally forms a solid mass. Y.P.M. 19452. Same faunule as that of figure 20.

ADDENDA

Yale Peabody Museum Bulletin number 11. Plate 7, figs. 16 and 17 (A2)



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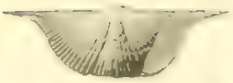

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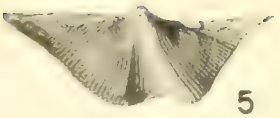

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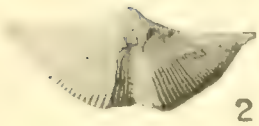

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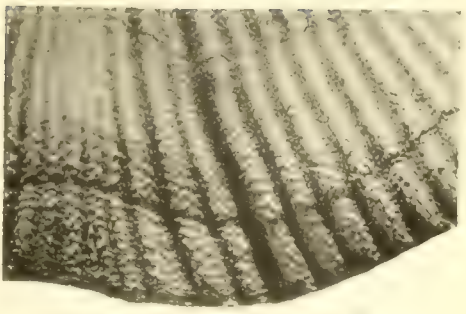

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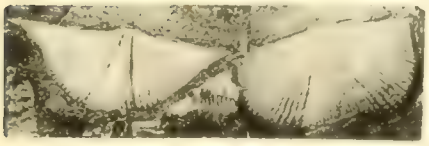

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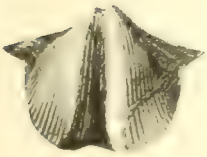

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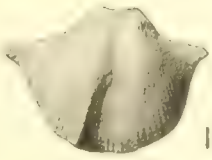

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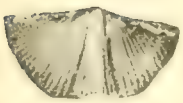

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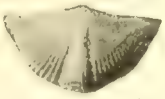

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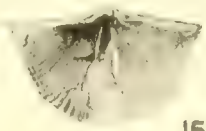

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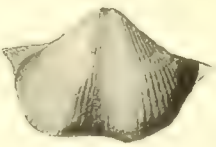

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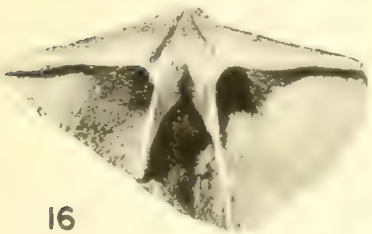

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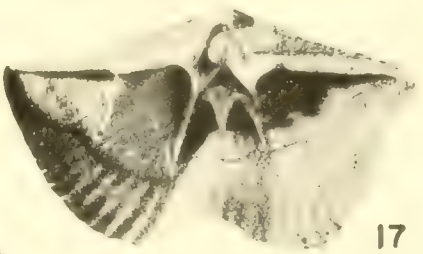

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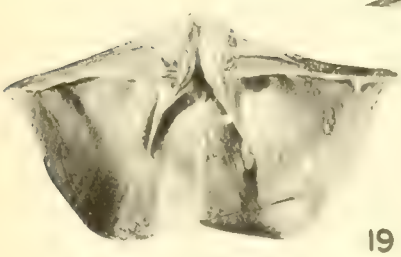

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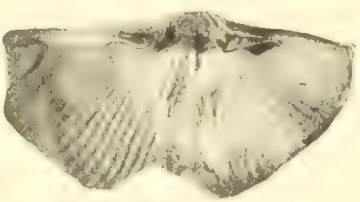

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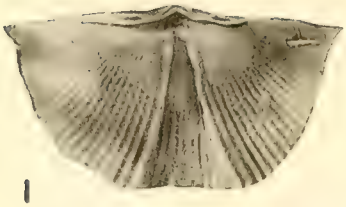

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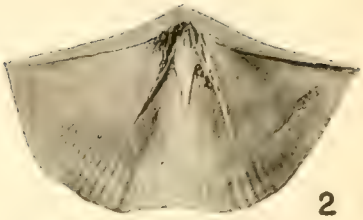

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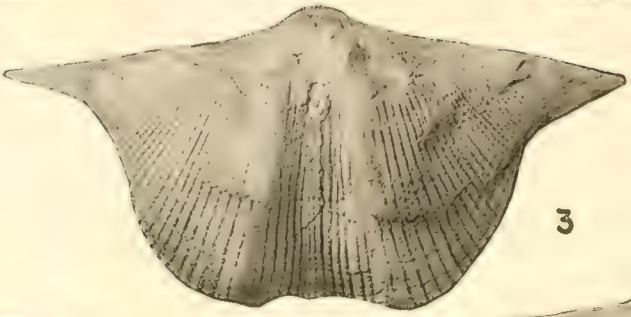

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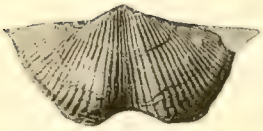

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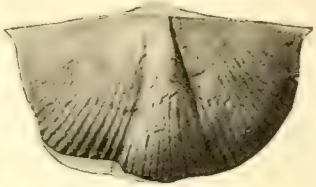

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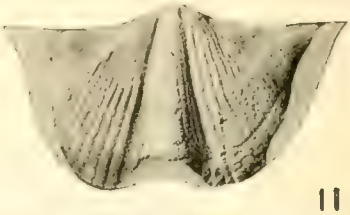

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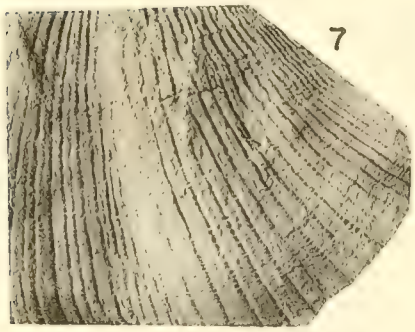

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PLATE 8

Cyrtospirifer tionesta n. sp. . . . p. 31

Fig. 1. Plastoparatype. Brachial valve interior, showing dental sockets and buttress plates. Y.P.M. 19454. Knapp formation, basal bed. Highway west of Riceville, Pa.

2. Plastoparatype. An exfoliated pedicle valve, some shell material remaining in the beak region, showing spatulate muscle scar, with long "apical callosity." Y.P.M. 19456. Saegerstown shale, upper part. Broadford Bridge, Meadville, Pa.

3. Paratype. Pedicle valve of a very large individual of typical shape. Y.P.M. 19457. Salamanca formation. Dennis Run, Tidioute, Pa. (Coll. E. I. Leith, 1931.)

4. Paratype. Pedicle valve of a young individual. Y.P.M. 19458. Tidioute shale. West end of bridge, Tionesta, Pa.

5, 6. Holotype. Posterior and ventral view of a pedicle valve of average size and shape. Y.P.M. 19459. Same faunule as the above.

7. Enlargement (x2) of surface of specimen shown in figure 6 to illustrate broad ribs and fine growth lines.

8. Paratype. Exterior of a brachial valve. Y.P.M. 19460. Amity shale, 1 mile south of Kinzua, Pa.

9. Paratype. View of cardinal area, showing vertical striation. Y.P.M. 19461. Oswayo shale. Dennis Run, Tidioute, Pa.

10, 11. Paratype. Posterior and dorsal views of a somewhat deformed brachial valve. Y.P.M. 19462. Same faunule as figure 9.

12. Paratype. Pedicle valves embedded in a sandstone matrix. The slender adductor muscle scars may be differentiated, in some. Y.P.M. 19463. Salamanca formation. Shale quarry at Lewis Run, Pa.

PLATE 9

Cyrtospirifer spicatus n. sp.; *"Spirifer" allegheniensis* Caster

Cyrtospirifer spicatus n. sp. . . . p. 32

Figs. 1, 2. Paratype. Posterior and ventral views of pedicle valve of a semicircular individual with very attenuate extremities. Y.P.M. 19464. Saegerstown shale, upper part. Stream section 1 mile north of Littles Corner on Highway 85, 8 miles northwest of Meadville, Pa.

3, 4. Plastoparatype. Posterior and ventral views of pedicle valve, showing wide cardinal area and pointed beak. Y.P.M. 19466. Amity shale. 3½ miles north of Meadville, Pa.

5. Paratype. Dorsal aspect of a brachial valve, showing numerous lateral costae. Y.P.M. 19467. Saegerstown shale. Creek section at Cambridge Springs, Pa.

6. Paratype. Natural cast of a pedicle valve in impure limestone matrix. Y.P.M. 19469. Chagrin shale, uppermost beds. Brandywine Creek, near Bedford, Ohio.

7, 8. Plastoholotypes. Exterior and interior of pedicle valve of a deformed specimen. Y.P.M. 19471a (exterior); 19471b (interior). Amity shale. 1 mile north of Corry, Pa. (Coll. E. I. Leith, 1931.)

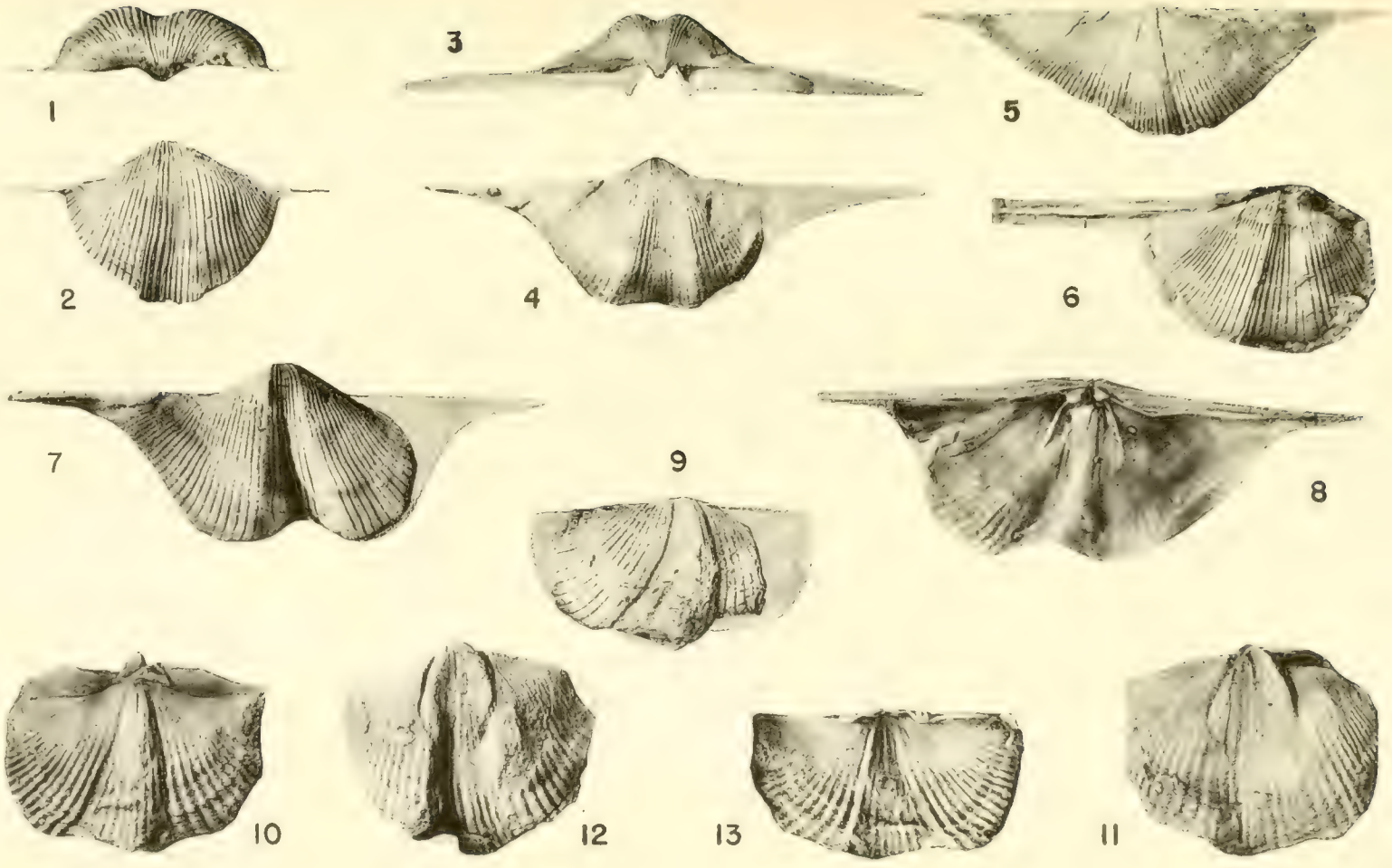
"Spirifer" allegheniensis Caster

Fig. 9. Plastohomotype. Part of a brachial valve, showing broad and few costae, rounded fold. Y.P.M. 19473. Cattaraugus formation, lower part (sandstone bed). Road cut 2 miles southeast of Humphrey, N.Y.

10, 11. Homotype. Dorsal and ventral views of a natural cast, showing restricted dental lamellae, muscle scar, subcircular shape, and few large ribs. Y.P.M. 19474. Corry sandstone. Roadcut 1 mile south of Garland, Pa.

12. Homotype. Ventral view of another pedicle valve, natural cast. Y.P.M. 19475. Same faunule as above.

13. Plastohomotype. Brachial valve interior. Y.P.M. 19477. Knapp conglomerate. Smith School junction, Warren, Pa.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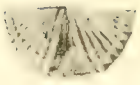

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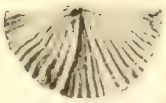

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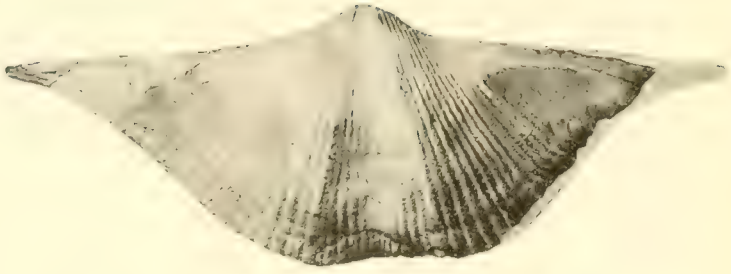

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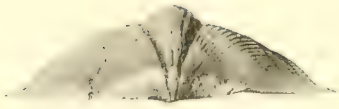

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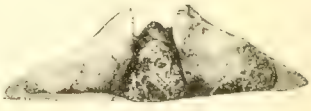

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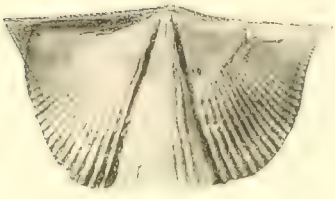

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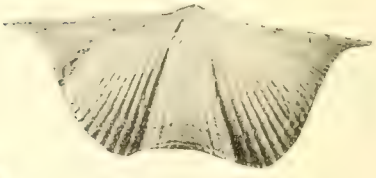

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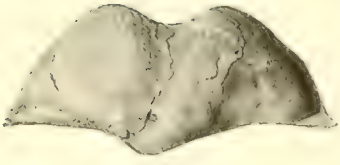

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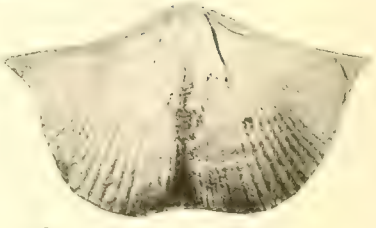

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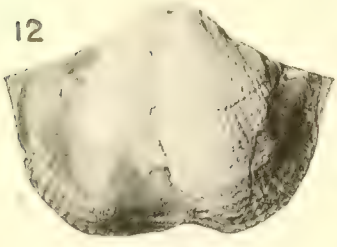

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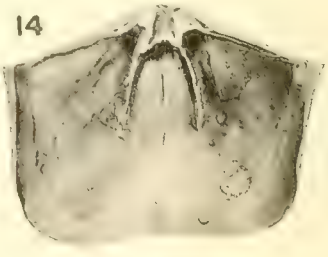

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PLATE 10

Cyrtospirifer inermis (Hall); *Cyrtospirifer corriensis* n. sp.

Aberrant variety of *Cyrtospirifer*(?)

Fig. 1. Cast of brachial valve of an odd form. Y.P.M. 19479. Found only at one locale, Amity formation, in a thin sandstone bed. Cambridge Springs, Pa.

2. Cast of another brachial valve. Y.P.M. 19481. Same faunule as the above.

3. Cast of interior of a pedicle valve, similar variety as the last two. Y.P.M. 19483. Same faunule as the above.

Cyrtospirifer inermis (Hall) . . . p. 24

Fig. 4. Plesiotype. Pedicle valve of a very large, wide form of the type found in the upper part of the Canaseraga sandstone. Y.P.M. 19484. Stephens Creek, near Hornell, N.Y.

Cyrtospirifer corriensis n. sp. . . . p. 33

Figs. 5, 6. Paratype. Posterior and dorsal views of a brachial valve, showing well-defined, high fold. Y.P.M. 19485. Amity shale, Cambridge Springs, Pa.

7. Paratype. Cardinal area of a natural cast. Y.P.M. 19486. Amity shale. 3½ miles south of Irvine, Pa.

8. Paratype. Natural cast of interior of an obese brachial valve. Y.P.M. 19487. Same faunule as above.

9. Paratype. Dorsal view of another brachial valve Y.P.M. 19488. Saegerstown formation. Bradford Bridge, near Meadville, Pa.

10. Paratype. Partly exfoliated pedicle valve, showing converging dental lamellae. Y.P.M. 19489. Same faunule as above.

11, 12, 13. Holotype. Posterior, ventral, and side views of a typical pedicle valve. Y.P.M. 19490. Amity shale. 1 mile north of Corry, Pa.

14. Plastoparatype. Pedicle valve interior, showing delthyrial plate, converging dental lamellae, and elongate muscle scar with fairly prominent adductor scar. Y.P.M. 19491. Same faunule as figure 7.

PLATE 11

Cyrtospirifer warrenensis n. sp. . . . p. 35

Fig. 1. Paratype. Brachial valve. Y.P.M. 19492. Corry sandstone. Sill Run, Warren, Pa. (Coll. E. I. Leith, 1931.)

2. Plastoparatype. Part of a brachial valve interior, showing dental sockets. Y.P.M. 19494. Salamanca formation. Asylum quarry, North Warren, Pa. (Coll. E. I. Leith, 1931.)

3. Plastoparatype. Pedicle valve, showing bifurcation in sinus. Y.P.M. 19496. Amity shale. 1 mile north of Corry, Pa.

4. Paratype. Brachial valve of a large individual. Y.P.M. 19497. Same locale as the above.

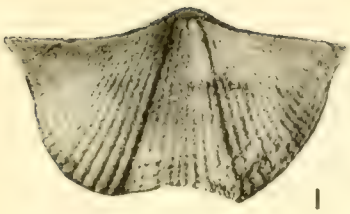
5, 6. Holotype. Ventral and side views of a pedicle valve. Y.P.M. 19498. Same locale as the above.

7. Plastoparatype. Latex impression of pedicle valve interior, showing typical, large, broad muscle scar, with anterior undulations. Y.P.M. 19500. Same locale as the above.

8. Plastoparatype. Interior, along the hingeline, showing tooth arrangement, dental lamellae, large crural plates, and cardinal process. Y.P.M. 19502. Salamanca formation. Asylum quarry, North Warren, Pa. (Coll. E. I. Leith, 1931.)

9. Plastoparatype. Pedicle valve interior, showing "apical callosity" and faintly radially striate muscle scar. Y.P.M. 19504. Same faunule and collection as the above.

10. Plastoparatype. Pedicle valve of an individual with a very high cardinal area. Y.P.M. 19506. Amity shale. 3½ miles south of Irvine, Pa.



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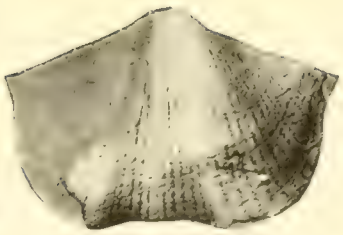

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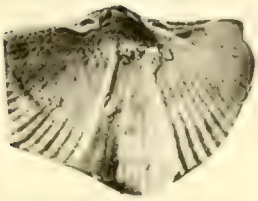

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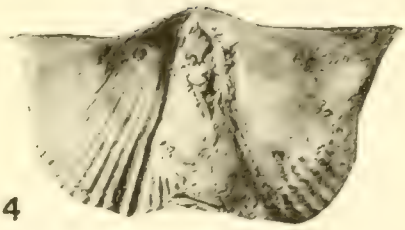

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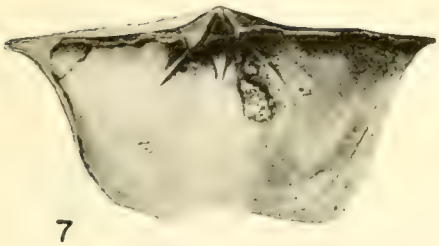

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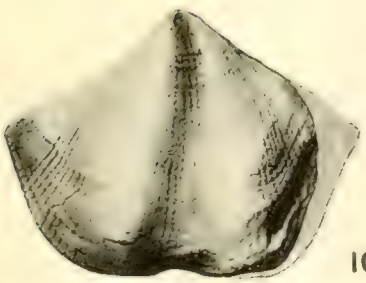

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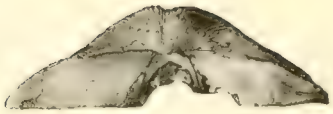

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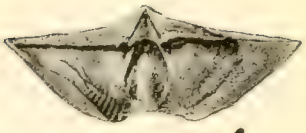

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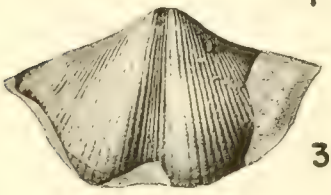

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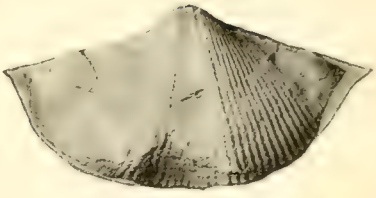

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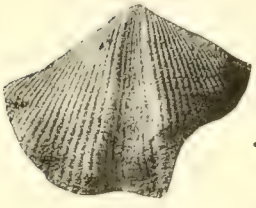

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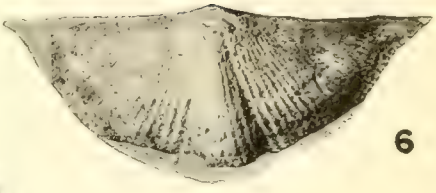

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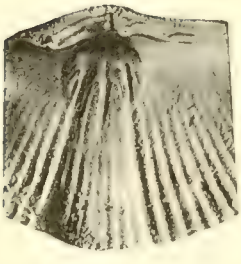

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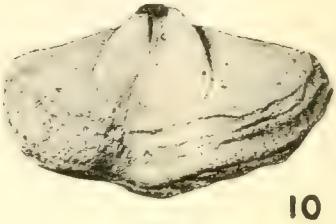

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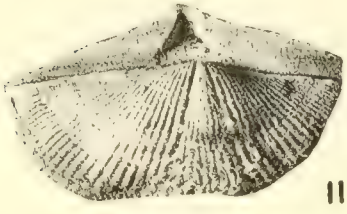

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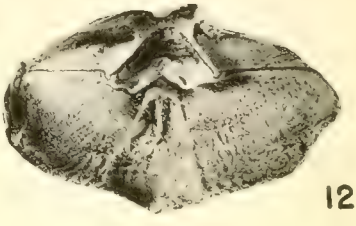

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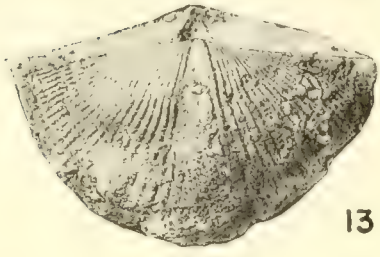

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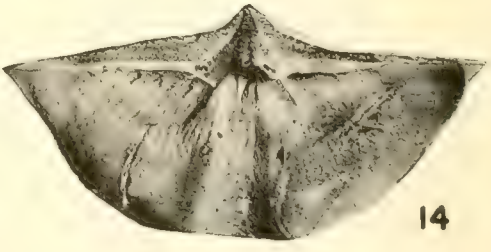

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PLATE 12

Cyrtospirifer oleanensis n. sp. . . . p. 36

Figs. 1, 2, 3. Plastoparatype. Posterior, side, and ventral views of latex impression of a pedicle valve, showing bifurcation in sulcus. Y.P.M. 19508. Corry sandstone, Grand Valley, Pa.

4. Plastoparatype. Interior of pedicle valve of a young individual. Y.P.M. 19510. Oswayo shale. Highway ¼ mile west of Ludlow, Pa.

5. Paratype. Pedicle valve, somewhat crushed in front. Y.P.M. 19511. Oswayo shale, basal "coquinite" bed. Highway at Flatiron Rock, Olean Rock City, N.Y.

6. Paratype. Brachial valve. Y.P.M. 19512. Same faunule as above.

7. Plastoparatype. Pedicle valve and sinus, showing bifurcating costae. Y.P.M. 19514. Oswayo shale. Flatiron Rock, Olean Rock City, N.Y. (Coll. E. I. Leith, 1931.)

8. Plastoparatype. Brachial valve and fold. Y.P.M. 19516. Same locale and collection as the above.

9. Plastoparatype. Enlargement (x2) of the muscle scar in the brachial valve. Y.P.M. 19518. Same locale and collection as the above.

10, 11, 12. Holotype. Natural cast, and plastoholotypes of the brachial valve and of the hinge area of the same individual. Note restricted dental lamellae, subcordate muscle scar, prominent dorsal muscle scar, and large crural plates. Y.P.M. 19519, 19520. Same locale and collection as the above.

13. Plastoparatype. Dorsal view of the cast of another shell of typical shape. Y.P.M. 19522. Same locale and collection as the above.

14. Plastoparatype. Pedicle valve interior, showing very brief dental lamellae and the cardinal area. Y.P.M. 19524. Same locale and collection as the above.

PLATE 13

Cyrtospirifer leboeufensis n. sp.; *Cyrtospirifer lobatimusculus* n. sp.

Cyrtospirifer leboeufensis n. sp. . . . p. 37

Fig. 1. Plastoparatype. Brachial valve, showing dental sockets. Y.P.M. 19526. Amity shale. 1 mile north of Corry, Pa.

2, 3, 4. Paratype. Posterior, side, and ventral views of an exfoliated pedicle valve, showing convergent dental lamellae. Y.P.M. 19527. Same faunule as the above.

5. Plastoparatype. Interior of a small pedicle valve, showing prominent striation of muscle scar, and subparallel dental lamellae. Y.P.M. 19529. LeBoeuf (Panama) sandstone. Quarry at LeBoeuf, Pa.

6. Plastoparatype. Pedicle valve of typical shape. Y.P.M. 19531. Same faunule as the above.

7, 8. Plastoholotypes. Exterior and interior of the same pedicle valve. Y.P.M. 19533a and 19533b. Same faunule as the above.

9. Plastoparatype. Pedicle valve of a young individual, showing early bifurcation in the sinus. Y.P.M. 19535. Same faunule as the above.

Cyrtospirifer lobatimusculus n. sp. . . . p. 38

Fig. 10. Paratype. Natural cast of a pedicle valve of typical size and shape, showing the distinctive, lobate muscle scar. Y.P.M. 19536. Orangeville shale. Iron bridge at Meadville, Pa. (Coll. E. I. Leith, 1931.)

11, 12. Plastoparatypes. Exterior and interior of the same brachial valve. Y.P.M. 19538, 19540. Knapp formation, basal bed. Yankeebush Road, Warren, Pa. (Coll. E. I. Leith, 1931.)

13, 14, 15. Plastoparatype. Posterior, side, and ventral aspects of a typical pedicle valve, showing bifurcation in sinus. Y.P.M. 19542. Same locale and collection as the above.

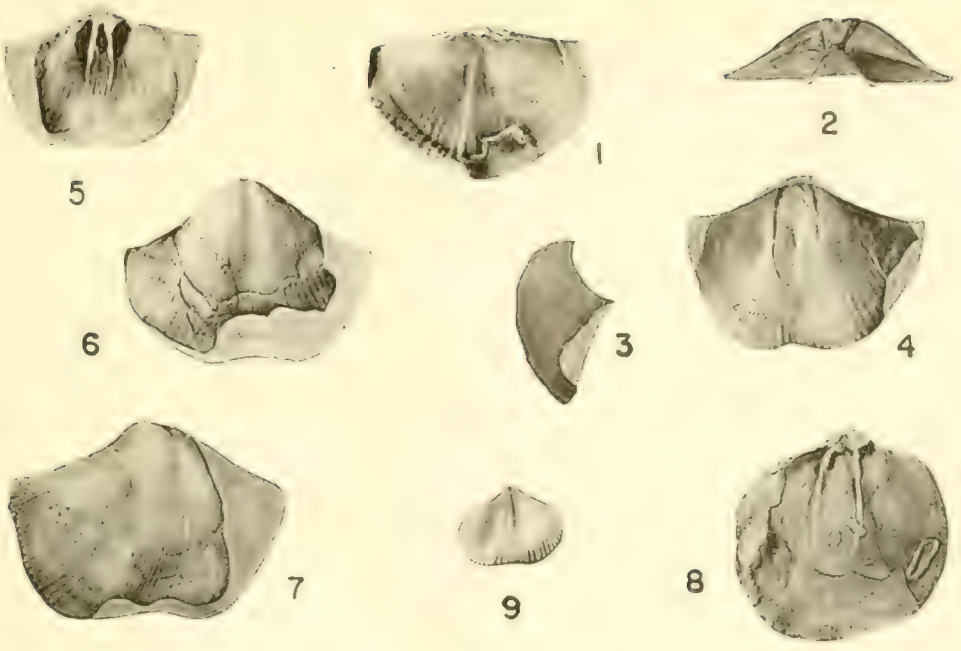
16. Paratype. Cardinal area of a natural cast. Y.P.M. 19543. Same locale and collection as the above.

17. Plastoparatype. Part of a pedicle valve, showing muscle scar. Same locale and collection as the above.

18. Plastoparatype. Pedicle valve interior, showing typical muscle scar. Y.P.M. 19547. Same locale and collection as the above.

19. Holotype. Natural cast of another interior of a pedicle valve of typical size and shape. Y.P.M. 19548. Same locale and collection as the above.

20. Plastoparatype. Brachial valve, showing broad costae. Same locale and collection as the above.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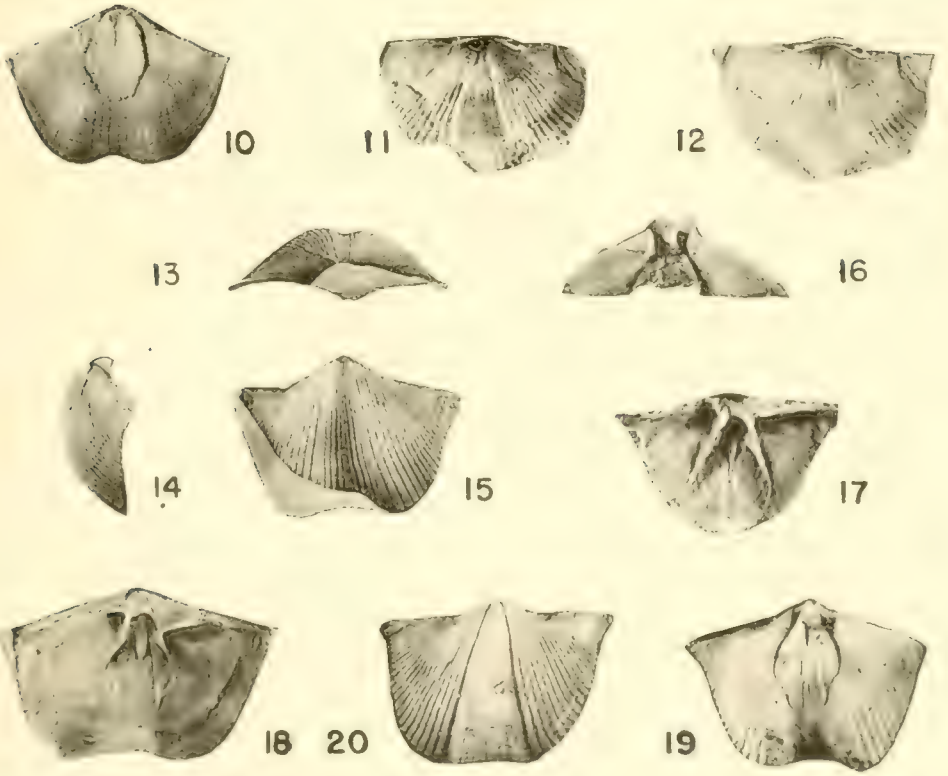
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